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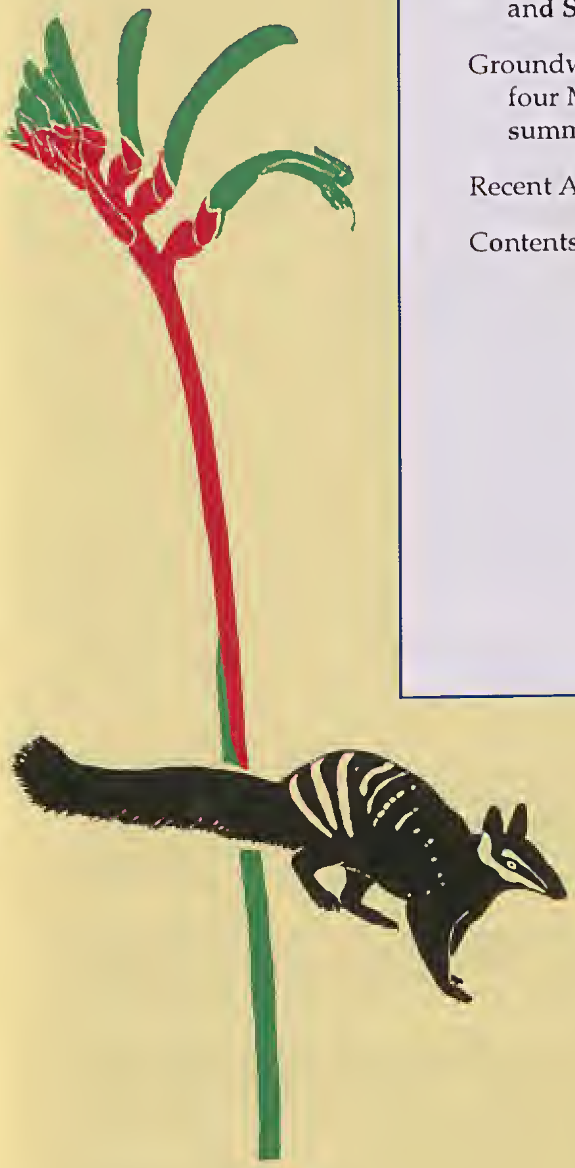

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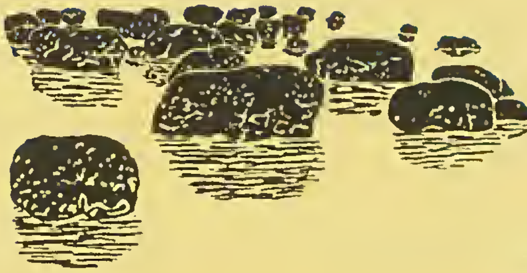

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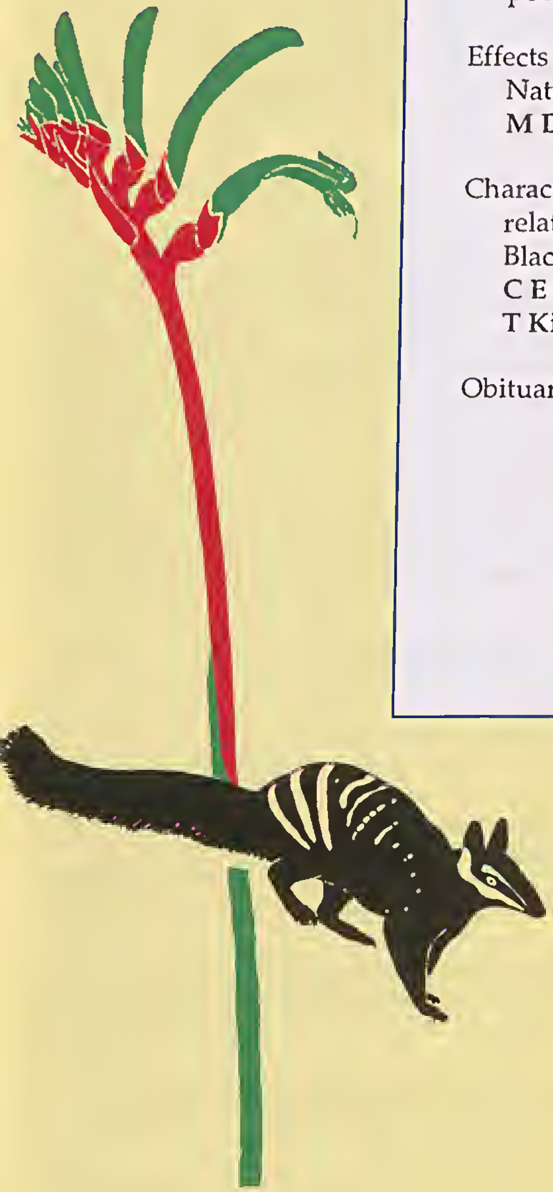

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The western bearded dragon, *Pogona minor* (Squamata: Agamidae): An early lizard coloniser of rehabilitated areas

S A Thompson & G G Thompson

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(Manuscript received March 2002; accepted August 2002)

Abstract

We investigated why the western bearded dragon (*Pogona minor)* is an early coloniser of rehabilitated waste dumps in the mining area around Ora Banda, Western Australia. The daily distance travelled for 19 (14 female and 5 male) *P. minor*, measured using nylon thread spools attached to the lizard's tail, was 115 m. This corresponded to a mean linear distance moved of 68 m. Our data suggest that *P. minor* are one of the first species of reptiles to colonise mine site rehabilitation areas because they move appreciably greater daily distances than other agamid lizards, are spatially widely-foraging, frequently forage in or use saltbush (*Atriplex* spp) and bluebush (*Maireana* spp) as basking sites, regularly traverse open areas, readily move up and down steep slopes, and eat bull ants which are generally present on rehabilitated sites. *Pogona minor* also have a high reproductive potential and show no obvious aversion to mine sites as oviposition locations. *Pogona minor* eggs incubated at 27 °C took an average of 64 days to hatch, the mean snout-to-vent length was 36.1 mm and the mean mass was 1.74 g.

Keywords: Western bearded dragon, *Pogona minor*, daily distance travelled, recolonisation, rehabilitated mine site, reproduction

Introduction

Although western bearded dragons (*Pogona minor*) are a common and conspicuous agamid lizard, particularly in spring when they are often seen on country roads, little is known about their daily movements or their biology (Greer 1989). *Pogona minor* is one of three species of bearded dragons (*P. minor*, *P. microlepidota* and *P. nullarbor)* in Western Australia (Aplin & Smith, 2001). Bearded dragons are medium-sized and stout in shape, with a well-developed row of spines on the head and along the sides of the body (Storr *et al.* 1983). The lizards in this study all had white mouths; elsewhere in the state some have yellow mouths.

Pogona minor is found in most habitat types in the Western Australian goldfields and is thought to be a widely-foraging, generalist feeder (Pianka 1986). Anecdotal evidence indicates that *P. minor* is one of the early colonising reptiles in mine site rehabilitation areas. It is not known if this is because of their widely-foraging behaviour with no apparent home range, or because they move greater distances in a day compared to other agamids, prefer the disturbed type of habitat often present in rehabilitated areas, or their relative high fecundity (based on multiple clutches in a season; Bradshaw 1981; B Jennings, University of Texas at Austin, personal communication) and recruitment forces juveniles into new areas.

The presence of *P. minor* on rehabilitated mine sites and the proportion of total species richness were used to determine whether this species is an early coloniser in rehabilitated mining areas. If *P. minor* is present and represents a higher proportion of the species in rehabilitated areas compared with the adjacent undisturbed areas, then this is evidence that they are one of the first species to colonise an area. Evidence of successful reproduction by species in a rehabilitated area would also provide evidence of successful colonisation into the area. Rehabilitated sites that are developing into self-sustaining functional ecosystems generally have less species than the adjacent undisturbed areas (Read 1999). Presuming an appropriate rehabilitation program is in place on the mine site, species richness will increase as species progressively move from the adjacent areas into the rehabilitated area (Fox & McKay 1981; Fox & Fox 1984; Fox 1990).

The aim of this research was to investigate the daily movement patterns of *P. minor* in the mining area around Ora Banda, Western Australia, to ascertain if there was a pattern to their daily movements (*e.g.* confined within an activity area), how far they travel in a day, which micro-habitats they frequent, and whether these data can shed light on why this species is an early coloniser in rehabilitated mine areas.

Methods

Pit-traps (alternating lines of 20 L PVC buckets and 600 x 150 mm PVC pipes, 5–6 m apart and joined by 300 mm high fly-wire drift fences) were used at rehabilitated mine sites and the adjacent undisturbed areas in the vicinity of Ora Banda (30° 22' S, 121° 03' E) to capture small vertebrates. Seventy two pit-traps (12 arrays of 6 lines) were placed on each of five rehabilitated waste dumps and 48 pit-traps (8 arrays of 6 lines) in the adjacent undisturbed areas. The pit trap arrays adjacent to the waste dumps are between 50 and 200 m away from the base of the waste dump. Pit traps were positioned in an additional six undisturbed areas (48 pit-traps each) during this period. Different habitats based on vegetation types were selected for each of the undisturbed areas. Although the undisturbed habitats varied in composition they can generally be characterised as Eucalypt-Casuarina-Mulga woodlands interspersed with *Acacia acuminata* shrublands. The rehabilitated waste dumps are less vegetated, generally with a sparse covering of chenopod shrubs (*i.e.* bluebush and saltbush) and large areas of bare ground. The waste dumps were rehabilitated in 1993, 1994, 1997 and 1998, and the fifth waste dump had a staged rehabilitation in 1992 and 1996.

Daily movements of adult *P. minor* were monitored between 13 and 29 September, 1 to 15 December 2001, and 11 to 23 January 2002, a total of 43 days. These lizards were caught by hand or in pit-traps and released at or near their place of capture within 10 minutes of capture. Lizards were weighed, snout-to-vent (SVL) and tail length measured, and individually numbered by toe clipping. Sex was confirmed by the eversion of hemipenes (for males) or the presence of eggs (for females).

A spool of white, double-stranded nylon thread (Penguin Thread Co, Victoria) was attached to the dorsal surface of the base of each lizard's tail with 35 mm grey, polyvinylchloride (PVC) electrical insulation tape. The attachment of the spool to the dorsal surface of the base of the tail was intended to minimise the possibility of the spool impeding movement. The free end of the thread was tied to a fixed object at the point of release. As the lizard moved away from this point the thread pulled away from the centre of the bobbin, leaving a white nylon thread on the ground indicating the path the animal had taken. Each nylon spool contained over 225 m of thread. If the nylon spool ran out, either the lizard was recaptured (and the spool replaced) or the insulation tape came off after a further 2–3 days, leaving the lizard unencumbered.

The daily movement patterns of 19 *P. minor* were recorded from the day after their release, by retrieving the nylon thread by hand, noting where the lizard had moved, and measuring the length of the nylon-thread trail. The lizards were handled and disturbed as little as possible, and there was no evidence to suggest that their distance travelled or their behaviour was affected by handling. A Universal Transverse Mercator (UTM) location for each *P. minor*, each day, provided a measurement of the linear distance moved for the previous day. UTM's were accurate to ± 4 m (Garmin GPSII Plus). The daily distance travelled, as measured by the length of the nylon thread, is referred to as the 'foraging distance', and the distance between UTM positions is referred to as the 'linear distance' travelled. The habitat traversed (*e.g.* number of bushes, log piles, ant mounds visited, *etc*) by each lizard was recorded when retrieving the nylon thread.

Most rehabilitated mining waste dumps around Ora Banda have steep sides with a flat or concave top. Vegetation on waste dumps generally consists of a high proportion of *Atriplex* spp and *Maireana* spp, often with little leaf litter, and many sites have large areas where the vegetation is sparse. Most have an apron of bare ground around the perimeter that colonising reptiles must cross to get onto the top of the waste dump. For most sites, the topsoil had been deeply ripped on the top and sides to stop water run-off, formation of gullies and erosion. Deep ripping creates a very uneven surface of linear mounds and furrows.

Three gravid females from the site were removed in early October and laid eggs that were incubated at 27.5 (± 1.0) °C in a mixture of vermiculite and water (1:1 by mass) to determine incubation period and neonate size at a known temperature.

Results

Pogona minor always represented a higher proportion of the reptile species richness in the five rehabilitated mining sites than in the adjacent undisturbed areas (1/14 species *vs* 1/33 species; 1/9 *vs* 1/25; 1/9 *vs* 1/17; 1/20 *vs* 1/25 and 1/17 *vs* 1/25). Because *P. minor* was present on all rehabilitated sites, even when the species richness was less than for the adjacent areas, we conclude that *P. minor* is one of the early reptile species to colonise rehabilitated mines sites in the Ora Banda area.

A spool was attached to five adult males (mass = 59.2 ± se 2.63 g; SVL = 125.8 ± se 3.15 mm) and 14 adult female *P. minor* (mass = 67.3 ± se 7.95 g; SVL = 128.9 ± se 2.42 mm). Nine lizards were recorded for six or more consecutive days, and we have 103 lizard-days of movement data. One lizard was found immobilised in a bush, caught by the nylon thread, on three occasions. Data for this lizard on the days for which its movement was impeded were not used in the analysis and are additional to the 103 days of data. There were no mortalities.

On some days, lizards did not move, and on some days the thread broke or ran out. Consequently we have three possible measurements of daily distance moved; a) distance travelled when the total distance moved was known (including when the lizard did not move and the thread did not break or run out) was 79.0 ± se 7.40 m (n = 79); b) distance travelled when the total distance moved was known but excluding those days when the lizards did not move away from their overnight position (and excluding days when the thread broke or ran out) was 114.6 ± 14.77 m (n = 90); and c) distance travelled on all days, including data where the thread broke, ran out or was dislodged, which was 111.7 ± 15.53 m (n = 103). The corresponding 'linear distances' are 41.2 ± 3.69 m, 68.3 ± 11.83 m and 66.8 ± 12.12 m. The length of thread when it broke or ran-out was greater than the mean for the known daily distance travelled ('foraging distance' = 186.4 ± 14.43 m and 'linear distance' = 123.4 ± 16.44 m, n = 11) so it can be assumed that the 114.9 m 'foraging distance' or 41.2 m 'linear distance' is an underestimate of the actual mean daily distance travelled by *P. minor*. The ratio of 'foraging distance' to 'linear distance' travelled was 1.68:1 for days when lizards moved and the total distance moved was known (*i.e.* moved with unbroken nylon thread).

Habitats traversed

Pogona minor regularly climbed into and over bushes and piles of logs (often created when earth-moving equipment had cleared vegetation for a road or track) during their daily movements. They often moved into the canopy of shrubs that were between 40 and 150 cm high, and the thread trail indicated in some instances that these lizards moved around (perhaps foraged) in these bushes. The mean number of bushes and log piles climbed over or foraged in each day when the lizard moved from its overnight retreat was 4.5 ± 0.61 (n = 317). This equates to one bush or log pile visited per 28.04 m of foraging distance travelled. Thread trails indicated that *P. minor* regularly crossed unvegetated areas or bare ground.

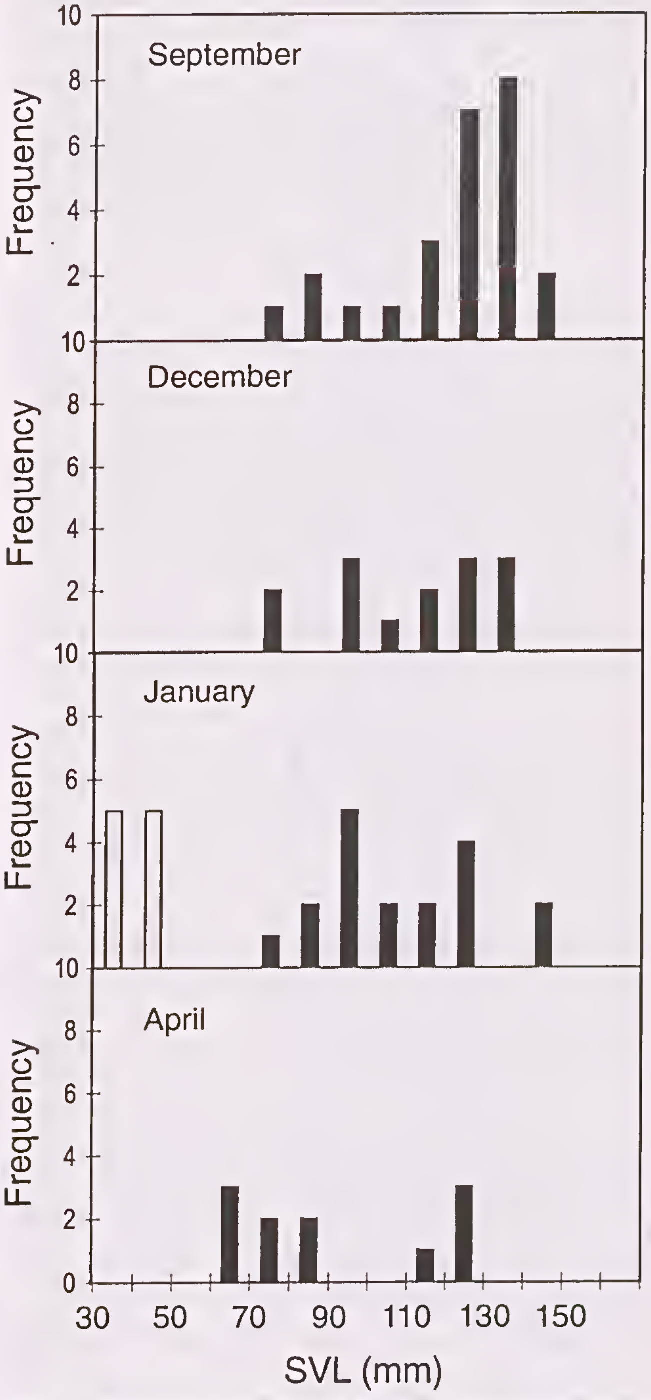

Figure 1. Snout-to-vent lengths of *P. minor* captured in pit-traps in the Ora Banda area during September, December, January and April showing the month which hatchlings (open bars) entered the population.

Reproduction

Three female *P. minor* were recorded as laying eggs in the field. One female dug two 'test' holes about 100 mm deep, one on 4 December and another on 6 December, and subsequently laid eggs later on 6 December. This female dug its burrow into the side of a mound so that the burrow was approximately horizontal. After laying her eggs she dug a vertical exit hole. The burrow entrance was ⌓ shaped and approximately 110 x 80 mm. The thread retrieved from the hole indicated that it was about 200 mm deep. A second *P. minor* dug its burrow on 9 December into flat ground and backfilled the hole so the disturbance was barely detectable. Again the thread left in the hole indicated the burrow was about 200 mm deep. Both of these egg chambers were excavated in April 2002 and seven hatched egg-shells were present in each burrow. Another female *P. minor* was recorded laying eggs in the field on 17 January. All egg burrows and 'test' holes were in open unvegetated areas, in full sunlight. Pit-trap data indicated that hatchlings were not present in early to mid December and first appeared in January (Fig 1). In January, hatchlings had a SVL in the range 35–50 mm; by April hatchlings had a 60–90 mm SVL. Two hatchling *P. minor* were caught in pit-traps on two waste dumps, suggesting that the colonising adults may be successfully reproducing in rehabilitated areas or very near by. No nesting burrows were actually observed on waste dumps.

Mean pre-oviposition body mass for three gravid females removed from the study site was 67.7 g. Oviposition occurred on 14, 16 and 19 October. Eggs incubated at 27.5 ± 1.0 °C took a mean of 64 days to hatch (Table 1). Neonates had a body mass of 1.74 ± 0.10 g, SVL of 36.1 ± 0.61 mm and tail length of 50.5 ± 2.10 mm (n =8). These captive-bred *P. minor* grew at the rate of 0.17 mm day^{-1} and 0.02 g day^{-1} for the first three months.

Table 1

Clutch mass, incubation period and neonate size for three clutches of *P. minor*. Measurements are mean (± se where applicable).

	Female A	Female B	Female C
Date of egg laying	14/10	16/10	19/10
Pre-oviposition body mass (g)	72.5	72.5	58.2
Post-oviposition body mass (g)	46.0	47.3	40
Clutch mass (g)	26.5	25.2	18.2
Relative clutch mass (%)	36.6	34.8	31.3
Clutch size	9	8	10
Mean egg mass (g)	2.9	3.2	1.8
Hatch dates	24/12	24 & 25/12	28-30/12; 1/1
Incubation period (days)	61	59, 60	70, 72, 74
Number of hatchlings	1	4	3
Mass of hatchling (g)	1.3	1.9 ± 0.03	1.7 ±0.21
SVL of hatchling (mm)	35	36 ± 0.82	37 ± 1.33
Tail of hatchling (mm)	49	49 ± 2.95	53 ± 4.48

General observations

Pogona minor appeared to have two patterns of movement based on information gleaned from the trail of nylon thread. They either moved about in what appeared to be a random pattern, foraging in logs, bushes or leaf litter that they encountered, or moved 'purposefully' in a particular direction. When the lizards were moving in a particular direction they would often go around or under bushes and logs in preference to through or over them. When these lizards were foraging the nylon thread was tangled and woven through the bushes, logs and leaf litter as they presumably searched the micro-habitat for prey. There were no obvious differences in the patterns of movement between males and females.

Pogona minor were often located early in the morning before they were active. They were normally found asleep under a bush in a shallow depression in the organic litter, on top of a saltbush (*Atriplex* spp) or bluebush (*Maireana* spp), or lying along a branch or twig in the canopy of larger shrubs (mostly *Acacia* spp). If the lizard was located during the warmer part of the day, it was frequently found on bare ground away from vegetation. In all cases when located during the day, *P. minor* made no attempt to run, and simply remained motionless. Lizards only moved away when disturbed (*i.e.* when recapture was attempted).

One individual lizard, on two occasions, systematically moved between bull-ant mounds (*Myrmecia* spp). On the first occasion, eight bull-ant mounds were visited in 112 m, and on the second occasion three bull-ant mounds were visited in 220 m. On both occasions the nylon thread indicated the lizard was passing through an area with little vegetation. Another captured lizard was found with a mouth full of chewed ants, confirming that *P. minor* eats these bull ants.

Pogona minor often returned to the same location multiple times, sometimes days apart. For example, lizard #2.16 returned 3 times to the same log pile 2 days apart (19/9–21/9 and 23/9–26/9). Another lizard (#3.11) was pit-trapped and released on 22 September and moved 132 m during the day before breaking the nylon thread (linear distance 70.5 m). This lizard was recaptured in a pit-trap, three days later (25/9) 25 m from its original location. The next day it moved 147 m in a similar direction to that which it had done on the 22/9 (linear distance of 74 m); and on the following day the lizard travelled 225m before running out of nylon thread within one metre of the previous day's release point. This lizard was not seen again. Another female lizard (#3.17) moved in a north-westerly direction for a period of three days with an accumulated 'foraging distance' of 303.9 m to a point where it laid her eggs. The following day she returned along the same route (within one metre most of the way), a 'foraging distance' of 239.2 m, before the thread ran out. Another *P. minor* (#4.8) crossed the same gap in a drift fence where there was a pit-trap three days in a row. This lizard also returned to the same bushes two days apart.

Pogona minor often moved over the deep rip lines and up and down the steep sides of rehabilitated waste dumps. Three different individuals (#2.6, #3.12, #3.15) moved between the sides of a waste dump and the top. Individual #2.6 was captured (17/9) on the top of the waste dump and moved down slope on the 19/9. It spent the next 14 days of observation moving around on the steep side of the waste dump. This lizard was previously caught on 7/4, 50m from the 17/9 capture location, indicating that it was still in the same vicinity after 5 months. *Pogona minor* #3.15 was first caught on top of a waste dump (30/11), moved down the slope and off the waste dump onto a top-soil storage pile (4/11), where two days later it laid eggs (6/11), then it moved into the adjacent undisturbed area (7/11) where it remained for two days until it returned (9/11) to the top-soil storage pile.

No lizards were observed to have walked along a drift fence or to have climbed out of a 20 L bucket or 150 mm PVC pipe used as the pit-traps. Three *P. minor* (#2.17, #3.12, #4.16) climbed over a drift-fence, one (#3.12) crossed the top of a 20 L bucket and two others (# 4.8, #3.15) crossed the top of a PVC pipe, indicating *P. minor* can easily cross a pit-trap line without being caught.

Discussion

Daily distances travelled by *P. minor* are large compared with most other lizards, and are typical of widely-foraging lizards. For example, the known daily distance travelled by the larger, widely-foraging goanna *Varanus gouldii* (mass = 478.7 g) was 111.6 m day^{-1} when measured using a spool-and-line tracking technique in a semi-urban environment (Thompson, 1992); when the total distance moved, excluding those days when the lizards did not move away from their overnight position and including data when the thread broke, ran-out or was dislodged, the distance travelled was 180.5 m day^{-1}. Sweet (1999) reported the arboreal, widely-foraging goanna *Varanus glauerti* (SVL = 213 mm, mass = 92 g) to move a mean linear distance of 33.7 m day^{-1} in western Arnhem Land, Northern Territory. This is much less than that of the slightly larger, arboreal and widely-foraging goanna *Varanus tristis* (male SVL = 255 mm, mass = 228 g, 187 m day^{-1}; female SVL = 255 m, mass = 249 g, 100 m day^{-1}) in the Great Victoria Desert, or the slightly longer, *Varanus glebopalma* (SVL = 265 mm, mass = 179 g) living on the escarpment of western Arnhem Land that moved a linear distance of 70.1 m day^{-1}. So, *Pogona minor* travelled a linear daily distance comparable with that of *V. glauerti* but less than that of the appreciably larger varanids. The slow-moving, sit-and-wait, ant-eating agamid *Moloch horridus* generally travelled a greater linear distance per day in the Great Victoria Desert (mean for males = 67 m day^{-1}, SVL = 78.7 mm, mass = 31.2 g; mean for females = 32 m day^{-1}, SVL = 91.0 mm, mass 45.5 g; Pianka *et al.* 1998) than *P. minor* at Ora Banda. The similar size, sit-and-wait, agamid *Lophognathus gilberti*, on the perimeter of Lake Kununurra, confines its daily movements to a much smaller area than *P. minor* with the result that the linear distance travelled in a day is much less than that for the *P. minor* (Thompson & Thompson, 2001). Some small agamids confine their daily movements to an activity area around a couple of burrows or retreats that they use on a regular basis (*e.g. Ctenophorus ornatus*, *C. inermis*, *C. maculosus*, Bradshaw, 1965; Mitchell, 1973). The 'linear distance' moved by these lizards is much smaller than that of *P. minor*. It can therefore be concluded that the daily distance moved by *P. minor* is generally greater than that moved for other lizards of a similar size.

The return of *P. minor* to previously used retreats and foraging sites suggests that they have a good spatial knowledge of their area, and their movement patterns are not random. Some *P. minor* foraged in confined areas, others moved in varying directions across the terrain, and others moved in a consistent direction for a number of consecutive days. Movement in a consistent direction despite walking around obstacles (shrubs, logs, *etc*) for one or more days suggested there was some 'purpose' or destination for the direction of movement. This 'purposeful' movement was not related to capture and processing.

Our intensive pit-trapping program at 11 sites for a period of seven days during September and December 2000; January, April, July, September and December 2001; and January 2002 (approximately 45 000 pit-trap days in total) only resulted in a single recapture of an adult *P. minor* between field trips, suggesting low site fidelity. However, we caught a single female *P. minor* (#2.6) in September within 50 m of where it was caught in the previous April, suggesting that this individual had remained in the vicinity. It might not have moved if these lizards have an activity area in which they forage over an extended period, or if it was inactive during the cooler winter months. Perhaps *P. minor* restrict their movements to an activity area, and our low recapture rates are due to their avoidance of pit-traps, as spooling showed. Additional data are necessary to ascertain if *P. minor* confine their movements to an activity area over an extended period.

Studies of the spatial ecology of reptiles often use radio-transmitters to locate animals each day. As a consequence, linear distance moved rather than the actual distance travelled is recorded, as it is not possible to determine accurately how far an animal actually travelled during the intervening period. Knowledge of the ratio of 'foraging distance' to 'linear distance' moved for *P. minor* enables an estimate to be made of daily foraging distances from linear displacement data collected using radio-transmitters. The ratio of 'foraging distance' to 'linear distance' for *P. minor* was about 1.68:1 for known distances travelled (excluding days when the lizards did not move from their overnight retreat) although the range varied markedly as some *P. minor* returned to their point of departure in the morning (ratio $\rightarrow \infty$), while others moved in almost a straight line for most of the day (ratio $\cong 1$).

Pianka (1986) reported that *P. minor* in the semi-arid, red sand-ridge, Great Victoria Desert eats ants, along with a wide variety of other invertebrates and plant material. One of the *P. minor* we monitored was frequently recorded on ant mounds, presumably feeding on ants (although it may have used these mounds as perches or basking sites) and another was caught with a mouth full of black bull-ants indicating that ants form part of the diet of *P. minor* in the Ora Banda area.

P. minor as an early coloniser

The conditions found on rehabilitated waste dumps (*e.g.* steep sides, lack of cover and leaf litter) would be a hostile environment for many small reptiles. The movement of *P. minor* from the top of the waste dumps and up and down the steep sides, across deep rip lines, and into the adjacent undisturbed area indicates that they will move across a variety of terrains to forage. This, together with their extensive daily movements, their willingness to move across unvegetated areas and climb steep slopes, and their propensity to forage widely and feed in dense low shrubs (*Atriplex* spp and *Maireana* spp) are likely reasons why it is an early colonising species in rehabilitated waste dumps. Interestingly, ants are also early colonisers of many rehabilitated mine sites (Majer 1989) and are a food source for *P. minor*.

Reproduction

Pianka (1986) reported *P. minor* to have a mean clutch size of 7.6 eggs and commit 19.5% of their body mass to a clutch. Greer (1989), in summarizing the available literature, reported clutch sizes for *P. minor* from 3–19, but mostly 5–8. The higher clutch sizes in Greer's data came from Bradshaw (1981) who reported a mean of 8.2 and a clutch size range of 5–19 eggs. More recently, Harlow *et al.* (2002) reported clutch sizes of 7, 8 and 9 for three *P. minor*, which are similar to the five (7, 7, 8, 9 and 10) that we recorded. Our measure of relative clutch mass (34.4%) is considerably higher than that reported by Pianka (1986; 19.5%) but similar to that reported by Harlow *et al.* (2002; 30.0%). We observed that the egg mass increases in the few days prior to parturition and there was a noticeable reduction in body tissue volume, particularly at the base of the tail. We presume that the shelled egg mass is increased by the uptake of water just prior to laying and this would account for the difference between the relative clutch mass values reported for oviducal and laid eggs. Given that some *P. minor* will double and triple clutch in a single summer (Bradshaw 1981; B Jennings, University of Texas at Austin, personal communication), these medium-sized lizards make a considerable energetic contribution to reproduction. The mean egg mass reported by Harlow *et al.* (2002) was smaller (2.02 g) than our eggs, although their neonates were generally heavier (mean 1.94 g) and longer (SVL = 38.3 mm). Harlow *et al.* (2002) reported the incubation period at 29 °C as 60.4 days (58–64), which is similar to those we incubated at 27.5 °C, and at 25 °C Harlow *et al.* (2002) reported they took a mean of 105.2 days (range 100–109) to hatch.

Field data and captive breeding records indicate the first hatchlings for the season appear either late in December or in early January. They have a SVL of 35–37 mm, body mass of 1.3–2.0 g when they hatch, and by April have increased their SVL to 65–85 mm with a corresponding body mass of 7–11.5g. The presence of hatchlings on waste dumps provides additional evidence this species can establish itself in rehabilitated areas.

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Reassessment of the vascular flora of Rottnest Island

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Abstract

A survey of the vascular flora of Rottnest Island, carried out between 1998 and 2001 with the aim of recording all native and introduced species, was compared with previous lists, and the nomenclature was reconciled and updated. A total of 246 native and introduced species have been recorded for the island, of which 196 species were found in 1998–2001. A survey in the late 1950s had recorded a similar total number of species (201) but the proportion of native species had dropped over the period between censuses from 62% in the 1950s to 58% in 1998–2001. Despite the relatively constant species total, the flora of Rottnest is dynamic, with 44 species known to have been present in the late 1950s not recorded at the end of the century, while 38 additional species were found in 1998/2001, giving a rate of turnover of 1% *pa*. In this paper, an annotated flora list of 246 recorded species is given as well as a list of 122 deleted names, with reasons for their exclusion from the flora list. Thirty-five cultivated species collected from outside of gardens, but which had not become naturalised, are listed separately.

Keywords: vascular flora, Rottnest Island, species turnover rate, immigration, extinction, island biogeography

Introduction

Rottnest Island has been the subject of intensive biological research due to its diversity of marine and terrestrial habitats, and its proximity to Perth-based research centres (Hodgkin & Sheard 1959; Bradshaw 1983; Huisman & Walker 1990; Wells *et al.* 1991; Walker & Wells 1996). As a result, much of the island's biodiversity has been documented.

It was during the 1950s that the first in-depth botanical explorations took place. McArthur (1957) compared the flora of Rottnest, Carnac and Garden Islands. Storr (1962) published a more complete annotated list of the Rottnest Island flora that formed the basis for subsequent floristic lists, specifically those of O'Connor (1977) and Frewer *et al.* (1985). These latter accounts accepted much of the information reported by Storr (1962) but included some changes in nomenclature and added a few new observations. Marchant & Abbott (1981) reviewed previous surveys and listed those species recorded for Rottnest and Garden Islands, and updated the nomenclature. Also available was a list of specimens from Rottnest Island lodged with the Western Australian Herbarium prior to 21st May 2001.

There were no major disturbance events on Rottnest Island from 1955 to the end of the twentieth century. The quokka (*Setonix brachyurus*) population remained at saturation level, fires were prevented or rapidly controlled, and the island was run as a conservation reserve for recreation and tourism. Under this regime tree species have been unable to regenerate naturally and a depauperate, sclerophyllous grassy heath has become the most widespread community on the island. This consists mainly of *Acanthocarpus preissii* and *Austrostipa flavescens* (Hesp *et al.* 1983), although the exotic geophyte *Trachyandra divaricata* has become an important constituent, having spread since the 1950s when it seldom occurred away from coastal dunes (Storr 1962).

Between 1998–2001 the Rottnest Voluntary Guides collected about 400 specimens of vascular plants, to establish the Rottnest Regional Herbarium (RRH). Identification by the Western Australian Herbarium of RRH specimens provided the basis for reconciling previously published lists, and enabled the size and composition of the flora to be re-assessed. This paper thus provides the first specimen-based list of the vascular plants of Rottnest Island.

Methods

All native and naturalised vascular species were targeted for the Rottnest Regional Herbarium, including aquatic angiosperms from the salt lakes, freshwater swamps and surrounding ocean. The plants of two islets off Rottnest Island, Dyer and Green, and Little Island in Lake Baghdad, were included. Cultivated trees and shrubs growing outside (but not inside) fenced gardens were also collected. All major habitats including the Settlement, woodlands, salt lakes, swamps, heathlands, and coastal areas were visited several times, at different seasons. Efforts were made to include differing topographical features within these areas, such as hills, rocky outcrops, swales and headlands.

Forty volunteers took part in the earlier collecting sessions and a total of approximately 500 person hours was spent in collecting specimens. The surveys were intended to cover as much of the island as was feasible in the time available. There was no formal grid survey pattern established nor were quadrats or transects included in the survey. All previously listed species were targeted, and recorded source areas were searched. At the time of collecting, details of each plant and its provisional identification, habitat, and locality were noted. Latitude and longitude were estimated from a photocopied aerial photograph on which a grid had been superimposed. The soil type and the nature of the vegetation in which the collected plant was growing were also recorded.

Each collection consisted of two specimens, one of which was submitted to the WA Herbarium for identification. These specimens were retained, apart from those of cultivated species that had not become naturalised. The Rottnest Regional Herbarium retained the duplicate specimens of all species collected. Where the size of the specimens made collection impracticable (*e.g.* palm trees) photographs were used. This collection, including photographs, is lodged with the Rottnest Island Authority. A colour photocopy was taken of one pressed specimen (or photograph) for each species in the collection and these are held by the Rottnest Island Authority for public reference.

We compiled a comprehensive list with current nomenclature of all species recorded for Rottnest Island, and attempted to reconcile it with all previous floristic lists. Our list included cultivated species that had become naturalised. We use the term 'naturalised' in a broad sense to include species in the colonisation phase that are starting to multiply on Rottnest without human intervention, and those in the naturalisation phase that have reproduced for several generations (Groves 1986).

Nomenclature was based on the WA Herbarium identifications of the specimens collected in the recent survey, supported by details in Paczkowska & Chapman (2000) or occasionally 'FloraBase' (Western Australian Herbarium, http://www.calm.wa.gov.au/science/florabase.html) and, in the case of some exotic taxa, by Bodkin (1993). Authors were not included but are available from the above references. Common names are taken from Paczkowska & Chapman (2000), and for orchids from Hoffman & Brown (1992). A second list was compiled for deleted names, annotated with reasons for their deletion from the Rottnest list or change in taxonomic status. Another list was compiled for species that had been cultivated outside gardens but had not become naturalised. These species are of historical and aesthetic importance on the island, and some may naturalise in the future.

Turnover of species between the two censuses (late 1950s, and 1998–2001) was investigated. It is difficult to assess turnover, because of the problems of measuring actual immigration and extinction rates, as noted by Sauer (1969) and Abbott (1983), because collections cannot be considered complete. Nilsson & Nilsson (1985) examined census efficiency and turnover when recording vascular plants on islands, and concluded that efficiency correlates positively with the time spent in taking the census, and negatively with island area. Even standardised searches by professional botanists recorded only 79% of the best estimate and the authors concluded that at most only 1% of the vascular plant species present on an island becomes extinct annually (Nilsson & Nilsson 1985). Whittaker (1998) noted that most turnover studies are in fact merely rates of changes in lists (as is this survey), and that turnover figures can be distorted by 'crypto-turnover' (exclusion of species that both immigrated and became extinct between surveys), and 'pseudo-turnover' (incomplete censuses).

Nevertheless, an assessment is made here using the available information. Turnover is taken as a combined effect of species 'extinction' and 'immigration'. A species was listed as extinct if it had been recorded previously, but was not listed in the latest census. Similarly the term 'immigrated' is applied to species recorded in the recent survey, but not previously. Turnover, immigration and extinction rates are calculated as suggested by Abbott (1977) and Abbott & Black (1980); rate of turnover = $200(I+E)/[(S_1+S_2) . (t_2 - t_1)]$; extinction rate = $200(E)/[(S_1+S_2) (t_2 - t_1)]$; and immigration rate = $200(I)/[(S_1+S_2) . (t_2 - t_1)]$; where E is the number of species that were presumed extinct, I is the number of species that immigrated, $(S_1 + S_2)$ is the sum of the number of species recorded at the two censuses, and $(t_2 - t_1)$ is the time elapsed between the two censuses. For the purposes of this survey, we assumed that 42 years elapsed ($t_1 = 1958$ and $t_2 = 2000$).

Some nomenclatural problems could not be resolved with certainty and these are addressed under 'taxonomic issues' in Appendix 1.

Results

A total of 196 vascular plant species was recorded for Rottnest Island between 1998 and 2001 (Table 1). The majority, 113 (58% of the total), were native species and 83 (42%) were introduced. The total comprised the 184 species collected for the RRH, five species recorded by other researchers since 1980 (*Avellinia michelii, Cerastium glomeratum, Drosera ramellosa, Oxalis pes-caprae* and *Ruppia tuberosa*), one seagrass (*Heterozostera tasmanica*) and six orchid species (*Eriochilus dilatatus, Leporella fimbriata, Microtis media, Prasophyllum giganteum, Pterostylis aspera* and *Pterostylis sanguinea*). Nine seagrass and eight orchid species are known for Rottnest (D I Walker, School of Plant Biology, University of Western Australia, personal communication; A Brown, Science and Information Branch, WA Dept of Conservation and Land Management, personal communication); only eight seagrasses and two orchids were collected for the RRH. Seagrasses and orchids can be difficult to collect, and were under-represented in both the RRH collection and Storr's (1962) census of Rottnest Island flora in the 1950s.

The comparable total number of species on the island in the late 1950s was 201 of which 124 (62%) were native species and 77 (38%) were introduced. This total consisted of 180 species recorded by Storr (1962), and 7 other species lodged with the WA Herbarium at the time of his survey (*Bromus madritensis*, a second *Comesperma* species, *Heliotropium curassavicum, Hydrocotyle blepharocarpa, Polypogon tenellus, Sarcocornia blackiana* and *Zygophyllum billardierei*). *Ricinus communis, Agave sisalana, Drosera ramellosa* and *Lobelia alata*, which were known to

Table 1

Native and introduced species, annual and perennial, recorded on Rottnest Island in the late 1950s and between 1998 and 2001.

	Late 1950s[1]			1998–2001[2]		
	Native	Introduced	Total	Native	Introduced	Total
Annual	29	54	83	22	50	72
Perennial	89	18	107	83	30	113
Annual or Perennial	6	5	11	8	3	11
Total	124	77	201	113	83	196

[1] *Centaurium, Comesperma, Conostylis, Rhagodia* and *Senecio* were counted as one species each.
[2] *Anagallis* and *Senecio* for which two varieties or subspecies were collected were counted as one species each.

be present before and after Storr's (1962) census, were assumed present, as were 4 orchid and 6 seagrass species that were not recorded in the 1950s.

The cumulative total number of vascular plant species recorded for Rottnest Island, including those that have become extinct, was 246 (*Anagallis, Eremophila, Rhagodia* and *Senecio* counting as one species each). One hundred and thirty-five were native species (55%) and 111 (45%) were introduced. These species are listed in Appendix 2.

Table 2

Species that became extinct or immigrated between the two censuses. (We acknowledge that some species listed could have been overlooked, misidentified or were dormant at the time of one or other census. Native species are perhaps less likely to have immigrated than aliens, and annuals less likely to have become extinct than perennials. Geranium molle, for example, was rediscovered in 2002).

Extinctions

Exotics

Agave sisalana
Arctotheca populifolia
Bromus madritensis
Carduus pycnocephalus
Centaurium pulchellum
Chenopodium murale
Crassula natans
Desmazeria rigida
Heliophila pusilla
Diplotaxis muralis
Ehrharta brevifolia
Geranium molle
Juncus bufonius
Leucojum aestivum
Lolium rigidum
Malva parviflora
Medicago polymorpha
Orobanche minor
Parentucellia latifolia
Pennisetum clandestinum
Reseda luteola
Silene nocturna
Sisymbrium orientale
Tetragonia decumbens
Trifolium suffocatum

Natives

Bulbine semibarbata
Centrolepis polygyna
Comesperma confertum
Comesperma integerrimum
Dodonea aptera
Heliotropium curassavicum
Hemichroa pentandra
Hydrilla verticillata
Juncus kraussii ssp *australiensis*
Malva australiana
Myosotis australis
Pelargonium littorale ssp *littorale*
Phyllangium paradoxum
Polypogon tenellus
Poranthera drummondii
Portulaca oleracea
Trachymene pilosa
Wurmbea monantha
Zygophyllum billardierei

Immigrations

Exotics (including species that naturalised)

Agave attenuata
Avellinia michelii
Caesalpinia gilliesii
Callitriche stagnalis
Casuarina glauca
Cerastium balearicum
Cirsium vulgare
Crassula glomerata
Crassula thunbergiana ssp *thunbergiana*
Cymbalaria muralis
Eragrostis curvula
Eucalyptus utilis
Euphorbia paralias
Ficus rubiginosa
Hedypnois rhagadioloides
Iris sp.
Lycopersicon esculentum
Malva dendromorpha
Melia azedarach
Minuartia mediterranea
Moraea flaccida
Narcissus tazetta
Nerium oleander
Oxalis pes-caprae
Raphanus raphanistrum
Rhamnus alaternus
Romulea rosea var *australis*
Solanum nigrum
Vulpia fasciculata
Vulpia muralis

Natives

Angianthus preissianus
Anthocercis littorea
Austrostipa elegantissima
Calandrinia aff *eremaea*
Centaurium spicatum
Lachnagrostis filiformis
Ruppia tuberosa
Schoenus nitens

Immigrations and extinctions

A few species had become extinct before the first flora list was published (Storr 1962). Two species were recorded by Preiss in 1839 but not since, *Amyema melaleucae* (see Frewer *et al.* 1985) and *Acacia truncata* (WA Herbarium specimen). *Heliophila pusilla, Reseda alba* and *Waitzia nitida* were only collected in about 1928, and *Sorghum bicolor* only in 1946–47 (WA Herbarium specimens).

There was a comparatively rapid turnover of species on the island between the late 1950s and late 1990s. Forty-four of the total 201 species (22%) known to have been present in the late 1950s were not recorded at the end of the century, while 38 additional species were found. The 82 species that either became extinct or immigrated are listed in Table 2.

The overall rate of turnover (immigrations plus extinctions) was almost 2 species per annum over the 42 years between the surveys, or 1% *pa*. Exotics had a turnover rate twice that of native species (0.7% species *pa* compared with 0.3% *pa*). The number of extinctions and immigrations was significantly higher for exotics than for native species ($\chi_1^2= 4.06$, $P <0.05$).

Overall, there was a tendency for native species to give way to exotics and for annuals to give way to perennials. The proportion of native species dropped from 62% to 58%, and the proportion of annuals dropped from 41% to 37%. The majority of native species recorded were perennial (73%, or 83 in a total 113 native species in the recent survey) but only a minority of the introduced species (36% or 30/83) were perennial.

The difference between the number of annuals that immigrated/became extinct compared with perennials was not statistically significant ($\chi_1^2= 2.86$, $P > 0.05$). Annuals had an extinction rate higher than the immigration rate (0.3% *pa* compared with 0.2% *pa*), while perennials had a higher immigration than extinction rate (again 0.3% *pa* compared with 0.2% *pa*).

Argyranthemum frutescens (marguerite) was recorded for the first time in 1986. This garden escape was eradicated at that time (Keighery 1986) and is a good example of successful eradication following rapid response to a naturalisation event. This species was the only recognised example of crypto-turnover in this study, being present between the two censuses but not recorded at either.

Deleted species names are provided in Appendix 3. Appendix 4 lists 35 exotic species cultivated outside gardens, which have not become naturalised.

Discussion

The revision necessary to achieve our Rottnest flora list involved the deletion of 122 species names, which are given in Appendix 3 together with explanatory notes. Half of the discarded names reflected simple taxonomic changes, with the older lists particularly requiring updating. Some of the revisions were complicated by two name changes. Others involved the splitting of one taxon into two; in cases where no material from Rottnest Island had been preserved by earlier collectors it was not possible to determine which of the two new categories had been recorded. A number of species listed by Storr (1962) and others who drew on his work appeared to have been misidentified. These were species that were not supported by herbarium specimens; where a species was not re-collected in the recent survey but a similar species was found, often in the location recorded previously, we assumed that the two species were the same. Nomenclatural problems that could not be resolved are addressed in Appendix 1.

The total number of extant species recorded changed little between the late 1950s and the end of the century, with 201 and 196 species respectively. The stability in the total number of species found on Rottnest Island over the past half century supports MacArthur & Wilson's (1967) theory of island biogeography, which states that the number of terrestrial species on islands tends to remain in equilibrium, with immigrations balancing extinctions. The total species number, according to their theory, is determined by the size of the island, the time since isolation and the distance from the nearest landmass. Comparable flora studies (Table 3) carried out on seven neighbouring, albeit much smaller islands, in the late 1950s showed that total species number did reflect the area of each island, as predicted by MacArthur & Wilson (1967). However, by the late 1990s most of the smaller islands had experienced drastic declines in biodiversity. This loss of species was associated with increasing numbers of nesting seabirds and invasion by *Malva dendromorpha* and other coprophilic alien plant species (Rippey *et al.* 2002). These influences were very restricted on Rottnest Island itself, but important on its satellite

Table 3

Number of plant species on islands off Perth in the late 1950s and the late 1990s (Garden Island is excluded from this comparison because no recent figures are available). Isolation is distance to mainland or nearest island.

	Area (ha)	Isolation (kilometres)	Species in late 1950s	Species in late 1990s	% change
Rottnest Island	1 900	17	201	196	-2
Carnac Island	16	8	82 a	62 b	-24
Penguin Island	12	0.7	74 a	76 c	+3
Seal Island	1.2	1	41 a	17 c	-59
Bird Island	0.9	0.3	31 a	14 c	-55
Dyer Island	0.6	1	18 a	17	-6
Shag Island	0.4	1.1	24 a	16 c	-33
Green Island	0.1	0.1	18 a	14	-20

[a] for 1959 (Abbott 1977); [b] for 1995 (Abbott *et al.* 2000); [c] for 1998 (Rippey *et al.* 1998)

islets, Dyer and Green Islands. A criticism of the theory of island biogeography (Sauer 1969) is the implication that equilibrium in the total number of species represents stability and characterises the community structure of an island. On Rottnest Island, the equilibrium between immigrations and extinctions masked the dynamic nature of the flora and considerable change in terms of species composition.

The vegetation of Rottnest Island contained a large proportion of exotic species, comprising 42% or 83 of a total 196 species in 1998–2001. The comparable figure for the Perth region was 27%, or 547 aliens in a total 2057 species (Marchant *et al.* 1987), and for Western Australia as a whole 11%, or 1052 in a total of 9640 (Paczkowska & Chapman 2000). The turnover rate of 2 species per annum (1.0% *pa*) between the two surveys was high, with exotic species proving particularly mobile.

Rottnest Island is fairly large (1900 ha) with varied habitats, but its flora is depauperate compared with the adjacent mainland. A grassy *Acanthocarpus* heath of low diversity is now the most widespread of the vegetation communities on the island, a situation not recorded before the 1950s. The greatest changes to the island's flora probably took place over the first 100 years of human settlement, when there was clearing, burning, tree cutting, and farming with the introduction of crop species and their attendant weeds and grazing by farm animals. The quokka population was suppressed by hunting. Storr's (1962) survey recorded the plant species on the island after this time, when farming had ceased, the quokka population had recovered, and the island had roads and a reliable water supply. Major disturbance factors had been absent for a decade, with the notable exception of the widespread fire of 1955.

Very few of the species introduced with the farming enterprises survived to the late 1950s. Storr (1962) recorded no agricultural annuals (their palatability and lack of dormancy presumably ensured their early demise) but the perennials *Ricinus* (Ferguson 1986) and *Agave* (Keighery 1988) persisted, as well as some long-lived fruit trees planted beside Garden Lake. Agricultural weeds presumably were abundant during farming operations, but few of these survived the harsh climate and quokka grazing. Some, such as *Avena barbata, Arctotheca calendula* and *Centaurea melitensis*, were recorded by Storr (1962), and were still present on the island in our survey but were rare. The tendency for annuals to give way to perennials is classic succession, following disturbance. However the present low prevalence of annuals may be due to their greater vulnerability to quokka grazing.

The vegetation of Rottnest Island has not had the same intensity of disturbance since Storr's (1962) census but conditions have not returned to the pre-European situation. First, there has been increasingly heavy traffic between the island and the mainland, attendant upon thousands of visitors each year (currently around 500 000 *pa*), which provided many opportunities for the introduction of new weed species. Secondly, wildfires that could revitalise the vegetation and temporarily reduce grazing by quokkas, have been infrequent and quickly controlled. Thirdly, the quokka population presumably has become so large that it dominates the makeup of the flora, in effect preventing the regeneration of palatable species, including the tree species (Pen & Green 1983).

Many of the plant extinctions on Rottnest Island may have taken place shortly after Storr's (1962) census in the aftermath of more recent fires and disturbance events. Certainly 29 of the 44 species that became extinct were known to have been rare in the late 1950s. Storr (1962) recorded 25 as such, mentioning that two of them (*Dodonaea aptera* and *Portulaca oleracea*) were known from only one specimen. A further 4 species were not recorded by Storr (1962) at all, but were known to have been on Rottnest Island from single WA Herbarium specimens collected in the late 1950s (*Bromus madritensis, Heliotropium curassavicum, Polypogon tenellus* and *Zygophyllum billardierei*). Significantly the majority of the species that became extinct were noted by Storr (1962) as being grazed or heavily grazed by quokkas.

Exotics made up an increasing proportion of the flora, and showed a particularly rapid turnover. These introduced species were concentrated in the developed areas, where they dominated the flora, but some were widespread across the island. The 35 exotic trees and shrubs listed in Appendix 4 include relics of nineteenth century market gardens and orchards, shading ornamentals for the benefit of twentieth-century tourists, and reafforestation species. These are of historic and landscaping or ornamental significance, as well as being potential sources for future naturalisations. Nine of the species that had been cultivated on the island became naturalised between the late 1950s and 1998–2001; specifically *Agave attenuata, Caesalpinia gilliesii, Casuarina glauca, Eucalyptus utilis, Ficus rubiginosa, Iris* sp, *Melia azedarach, Narcissus tazetta* and *Nerium oleander*. These are included in the comprehensive list of Rottnest flora (Appendix 2).

A number of introduced species were considered a threat to the vegetation of the island and have been targeted for eradication, including *Zantedeschia aethiopica, Euphorbia paralias, Ricinus communis, Rhamnus alaternus* and *Nicotiana glauca. Gomphocarpus fruticosus* is a noxious weed that was eradicated from all but one site, where it was retained because it was the only food plant on the island for the Wanderer butterfly (*Danaus plexippus*) and the native Lesser Wanderer (*Danaus chrysippus*) (Hay *et al.* undated).

Some of the species that immigrated or became extinct merit comment. *Pelargonium littorale* ssp *littorale* was 'widespread and abundant' in the 1950s according to Storr (1962), although subject to heavy grazing. This was not collected in 1998–2001; possibly it had been eaten out by quokkas. *Malva australiana*, which was recorded by Storr (1962) as common on the islets, could not be found, and has apparently been supplanted by the European tree mallow, *Malva dendromorpha. M. australiana* is now rare on the islands off Perth, persisting only on Carnac (Abbott *et al.* 2000) and Middle Shag Islands (Rippey *et al.* 2002). *M. australiana* and *M. dendromorpha* are palatable to quokkas and so do not occur on Rottnest itself, except for a clump of *M. dendromorpha* on the islet in Lake Baghdad. *M. dendromorpha* occasionally hybridises with *M. australiana*, an example of genetic pollution. The native *Hydrilla verticillata* was collected in 1955 from a small pool on the south east edge of Government House Lake and was identified by Storr (1962) as *Elodea canadensis*, an alien species that does not occur in Western Australia (Hussey *et al.* 1997). The habitat still exists, but *H. verticillata* has disappeared, and it is likely that it was eradicated because of its resemblance to *Elodea*, an declared alien species. One recent introduction of interest was *Euphorbia paralias* along beaches. This was probably introduced on boats, an inevitable event in view of its widespread distribution along the mainland coast south of Perth (Keighery & Dodd 1997).

The native *Anthocercis littorea* was recorded on Rottnest Island for the first time after a fire in 1997. Its seeds are hardcoated and can remain dormant until fire or disturbance of the soil cause germination (Powell & Emberson 1981; Haegi *et al.* 1982), yet this very conspicuous perennial species was not recorded during the botanical surveys after the 1955 fire, which included the site of the present specimen (500 m west of Barker Swamp). Birds are probably not responsible for bringing its seeds to the island, as the capsules are dry and the seeds are small, making them more suited to insect dispersal (L Haegi, Royal Botanic Gardens, Sydney, personal communication). It is possible that the seeds of this species have remained viable in the soil for many decades. Whatever its origin, this one plant is a true 'first record' for Rottnest of a coastal species that is common on the mainland (Rippey & Rowland 1995).

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APPENDIX 1

TAXONOMIC ISSUES

1. *Erythraea centaurium*
   E. centaurium as used by Storr and O'Connor was a misapplied name for *Centaurium erythraea* (Paczkowska & Chapman, 2000)
   C. erythraea has long been confused with *C. tenuiflorum* and *C. pulchellum*, both recorded for Rottnest Island.
   Centaurium is a very difficult genus and differences between closely related species are often very slight, making identification difficult.
2. *Lepidosperma* spp
   The taxonomy of the genus *Lepidosperma* is particularly complex and the boundaries between related taxa are not always clear. Such is the case between *L. squamatum* and *L. pubisquameum*. Only *L. gladiatum* and *L. pubisquameum* are included in the definitive list (Appendix 2).
3. *Didiscus pusillus* was listed by Storr (1962). Marchant & Abbott (1981) mention that *Trachymene pilosa* was previously known as *Didiscus pilosus*. In the absence of WA Herbarium vouchers, perhaps this could have been a pale *Trachymene coerulea*. Plants with white flowers certainly occur, and can be stunted in marginal sites. However *T. pilosa* certainly occurs on Garden Island, and could well have occurred on Rottnest Island. It is presumed extinct.
4. Names applied to samphires on Rottnest Island since 1962

Storr (1962)		O'Connor (1977)		Frewer (1985)		Rottnest Regional Herbarium
Arthrocnemum halocnemoides[1]	→	*A. halocnemoides*	→	*Halosarcia halocnemoides*	→	*H. halocnemoides*
Arthrocnemum arbuscula[1,2]	→	*A. arbuscula*	—	—	→	*Halosarcia indica*
Salicornia australis	→	*Salicornia quinqueflora*	↗	*Salicornia quinqueflora*	→	*Sarcocornia quinqueflora*
			↘	*Sarcocornia blackiana*	→	*Sarcocornia blackiana*

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[1] Storr's descriptions possibly transposed.

[2] This is a synonym of *Sclerostegia arbuscula* which is only known from the south coast. Probably an incorrect identification of *Halosarcia indica*.

Appendix 2

Flora list for Rottnest Island. The authority for nomenclature was Paczkowska & Chapman (2000) unless otherwise stated.

Explanatory notes:

1: listed by Storr (1962) or mentioned in Storr *et al.* (1959). This column represents the first flora census, late 1950s.
2: Listed O'Connor (1977)
3: Listed Marchant & Abbott (1981)
4: Listed Frewer *et al.* (1985)
5: Rottnest Regional Herbarium. This column represents the current flora census, 1998–2001
6: Vouchered specimens with the Western Australian Herbarium at 21.5.2001
*denotes introduced species; [...] signifies name/s used by previous author/s; ( ) authorities and general notes; X denotes a species not recorded by Storr or RRH but for which a specimen was lodged at the WA Herbarium at about the time of the census, or seagrasses or orchids (these can be difficult to collect so were poorly represented in censuses but were believed to be present on the island), or species recorded before and after the 1950s census or shortly before the 1998–2001 census and thus considered present at the time of the relevant census; ? denotes species recorded by Storr (1962) but not supported by a WA Herbarium voucher, which now may be either one of two species.

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	NOTES	COMMON NAME
Agavaceae	**Agave americana*	y	y		y	y	1986		century plant
Agavaceae	**Agave attenuata*					y		(Authority: Bodkin 1993)	
Agavaceae	**Agave sisalana*	X					1986-87	Present since at least 1940s, and eradicated 1987 (Keighery, 1988)	
Aizoaceae	*Carpobrotus virescens*	y	y	y	y	y	1998-99	[C *aequilaterus* - Storr, O'Connor]	coastal pigface
Aizoaceae	**Mesembryanthemum crystallinum*	y	y		y	y	1998-99	[*Cryophytum crystallinum* - Storr. *Gasoul crystallinum* - O'Connor]	common iceplant
Aizoaceae	**Tetragonia decumbens*	y	y	y	y			[*T. zeyheri* - Storr, O'Connor]. Possibly extinct	sea spinach
Aizoaceae	*Tetragonia implexicoma*	y	y	y	y	y	1839-1998	[*Tetragonia amplexicoma* - M&A, WA Herb]	bower spinach
Amaranthaceae	*Hemichroa pentandra*	y	y		y		1956	Collected only in 1956. Probably extinct	trailing joint weed
Amaryllidaceae	**Leucojum aestivum*	y	y		y			Naturalised at Bathurst Point from cultivated specimens. Apparently extinct	snowflake
Amaryllidaceae	**Narcissus tazetta*					y	1981-2000	First collected 1981	jonquil
Anthericaceae	*Thysanotus patersonii*	y	y	y	y	y	1920s-2000		twining fringe lily
Apiaceae	*Apium annuum*	y	y	y	y	y	1956-99	[*Apium australe* - Storr, O'Connor. *Apium prostratum* - M&A, Frewer]	
Apiaceae	*Daucus glochidiatus*	y	y	y	y	y	1956-99		Aust. carrot
Apiaceae	*Hydrocotyle blepharocarpa*	X				y	1956-2000		
Apiaceae	*Hydrocotyle diantha*	y	y		y	y	1999		
Apiaceae	*Hydrocotyle hamelinensis*	y	y	y	y	y	2000	[*H. tetragonacarpa* - Storr, O'Connor, M&A, Frewer, WA Herb]	
Apiaceae	*Hydrocotyle hispidula*	y	y	y	y	y	1999		
Apiaceae	*Trachymene coerulea* subsp *coerulea*	y	y	y	y	y	1972-98	[*Didiscus caeruleus* - Storr. *T. coerulea* - O'Connor, M&A, Frewer]. See taxonomic issues - appendix 1	Rottnest Island daisy
Apiaceae	*Trachymene pilosa*	y		y				[*Didiscus pusillus* - Storr]. See taxonomic issues	native parsnip
Apocynaceae	*Alyxia buxifolia*	y	y	y	y	y	1956-98		dysentery bush
Apocynaceae	**Nerium oleander*				y	y	1998	Naturalised from cultivated specimen	oleander
Araceae	**Zantedeschia aethiopica*	y	y	y	y	y	1987-98	Eradication target	arum lily
Asclepiadaceae	**Gomphocarpus fruticosus*	y	y		y	y	1986-98	[*Asclepias fruticosa* - Storr, O'Connor]	narrowleaf cottonbush
Asphodelaceae	**Asphodelus fistulosus*	y	y	y	y	y	1950-1998		onion weed
Asphodelaceae	*Bulbine semibarbata*	y	y		y			[*Bulbinopsis semibarbata* - O'Connor]	leek lily
Asphodelaceae	**Trachyandra divaricata*	y	y	y	y	y	1995-99	[*Anthericum divaricatum* - Storr]	S.A. onion weed
Asteraceae	Millotia myosotidifolia	y	y		y	y	2000	[M. *tenuifolia* - Storr, O'Connor, Frewer]. Only collection 2000	
Asteraceae	**Arctotheca calendula*	y	y	y	y	y	1999		capeweed
Asteraceae	**Arctotheca populifolia*	y	y	y	y			[*A. nivea* - Storr]. Presumed extinct	dune arctotheca

Asteraceae	**Argyranthemum frutescens*							Recorded 1986 (G. Keighery 1986) and eradicated	marguerite
Asteraceae	**Carduus pycnocephalus*	y	y	y	y			[*C. tenuiflorus* - Storr, O'Connor, Frewer]. Presumed extinct	slender thistle
Asteraceae	**Centaurea melitensis*	y	y		y	y	1956-2000		maltese cockspur
Asteraceae	**Cirsium vulgare*					y	2000	One collection 2000	spear thistle
Asteraceae	**Conyza albida*	y	y	y	y	y	1999	[*Erigeron canadensis* - Storr, O'Connor. *Conyza bonariensis* - M&A. *Conyza canadensis* - Frewer]	tall fleabane
Asteraceae	*Cotula australis*	y	y		y	y	1990-99		carrot weed, common cotula
Asteraceae	*Cotula coronopifolia*	y	y		y	y	1998-99		water buttons
Asteraceae	**Dittrichia graveolens*	y	y	y	y	y	1976-99	[*Inula graveolens* - Storr]	stinkwort
Asteraceae	**Hedypnois rhagadioloides*					y	1998		cretan weed
Asteraceae	**Hypochoeris glabra*	y	y	y	y	y			flatweed, smooth cat's ear
Asteraceae	*Leucophyta brownii*	y	y	y	y	y	1998-99	[*Calocephalus brownii* - Storr, O'Connor, M&A, Frewer]	cushion bush
Asteraceae	*Olearia axillaris*	y	y	y	y	y	1998-99		native rosemary, coastal daisy bush
Asteraceae	*Podotheca angustifolia*	y	y		y	y	1920s-99	[*Podosperma angustifolium* - Storr]	sticky longheads
Asteraceae	*Senecio lautus* subsp. *dissectifolius*	?X		?	?	y	1956-2000	[*Senecio lautus* - Storr, M&A, Frewer, RRH, WA Herb]. Where unvouchered, cannot determine which taxon was recorded	variable groundsel
Asteraceae	*Senecio lautus* subsp. *maritimus*	?X	y	?	?	y	1956-99	[*Senecio lautus* - Storr, M&A, Frewer, RRH, WA Herb]. Where unvouchered, cannot determine which taxon was recorded	coastal groundsel
Asteraceae	**Sonchus oleraceus*	y	y	y	y	y	1999		common sowthistle
Asteraceae	*Waitzia nitida*						1920s	Collected approx. 1920s. Presumed extinct	
Asteraceae	*Angianthus preissianus*					y	1999-2000	First collected 1999	
Boraginaceae	*Heliotropium curassavicum*	X					1959	Collected 1959. Presumed extinct	smooth heliotrope
Boraginaceae	*Myosotis australis*	y	y	y	y		1956	Only collected 1956. Presumed extinct	southern forget-me-not
Brassicaceae	**Cakile maritima*	y	y	y	y	y	1920s-99		sea rocket
Brassicaceae	**Coronopus didymus*	y	y		y	y	1987-99		lesser swinecress
Brassicaceae	**Diplotaxis muralis*	y	y		y		1956	One specimen 1956. Presumed extinct	wall rocket
Brassicaceae	**Heliophila pusilla*	y	y		y		1920s	One collection late 1920s. Presumed extinct	
Brassicaceae	*Hornungia procumbens*	y	y	y	y	y	1956-99	[*Hymenolobus procumbens* - Storr, O'Connor, M&A, Frewer]	oval purse
Brassicaceae	*Lepidium foliosum*	y	y		y	y	1999	Offshore islets only	leafy pepper cress
Brassicaceae	**Raphanus raphanistrum*					y		One specimen collected 1999	wild radish
Brassicaceae	**Sisymbrium orientale*	y	y	y	y			Presumed extinct	Indian hedge mustard
Caesalpinaceae	**Caesalpinia gilliesii*					y	1996-98	Naturalised from a cultivated specimen. Eradication target	
Callitrichaceae	**Callitriche stagnalis*					y	1999		common starwort
Caryophyllaceae	**Arenaria leptoclados*	y	y			y		[*A. serpyllifolia* - Storr, O'Connor]	
Caryophyllaceae	**Cerastium glomeratum*	y	y	y	y	X	1987	[*Cerastium viscosum* - Storr, O'Connor]	
Caryophyllaceae	**Cerastium balearicum*					y	1999		chickweed
Caryophyllaceae	**Minuartia mediterranea*					y	1995-99	First collected 1995	
Caryophyllaceae	**Polycarpon tetraphyllum*	y	y	y	y	y	1999		four leaf allseed
Caryophyllaceae	**Sagina maritima*	y	y	y	y	y	1987-99	[*S. apetala* - Storr, O'Connor, M&A, Frewer]	
Caryophyllaceae	**Silene nocturna*	y	y		y			Presumed extinct	Mediterranean catchfly
Caryophyllaceae	**Stellaria pallida*	y	y	y	y	y	1987-99	[*Stellaria media*: Storr, O'Connor, M&H, Frewer, RRH, WA Herb]	chickweed
Casuarinaceae	**Casuarina glauca*					y	2000	Naturalised from a cultivated specimen	
Centrolepidaceae	*Centrolepis polygyna*	y	y		y		1956	One collection 1956. Presumed extinct	wiry centrolepis
Chenopodiaceae	*Atriplex cinerea*	y	y	y	y	y	1920s-1998	[*A. paludosa* - Storr, O'Connor]	grey saltbush
Chenopodiaceae	*Atriplex isaditea*	y	y	y	y	y	1839-1999	[*A. cinerea* - Storr]	coast saltbush

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	NOTES	COMMON NAME
Chenopodiaceae	**Chenopodium murale*	y	y	y	y			Presumed extinct	nettle-leaf goosefoot
Chenopodiaceae	*Enchylaena tomentosa* var *tomentosa*	y	y	y	y	y	1998-99	[*E. tomentosa* - Storr, O'Connor, M&A, Frewer]	barrier saltbush
Chenopodiaceae	*Halosarcia halocnemoides* subsp *halocnemoides*	y	y		y	y	1978-98	[*Arthrocnemum halocnemoides* - Storr, O'Connor. *Halosarcia halocnemoides* - Frewer]. See taxonomic issues	shrubby samphire
Chenopodiaceae	*Halosarcia indica* subsp *bidens*	y	y			y	1956-98	[*Arthrocnemum arbuscula* - Storr, O'Connor] See taxonomic issues	
Chenopodiaceae	*Rhagodia baccata* subsp *baccata*	?	?	?	?	y	1998-99	[*R. baccata* - Storr, O'Connor, M&A, Frewer, RRH,WA Herb]. Where unvouchered, cannot determine which taxon was recorded	sea berry saltbush
Chenopodiaceae	*Rhagodia baccata* subsp *dioica*	?	?	?	?	?	1976	[*R. baccata* - Storr, O'Connor, M&A, Frewer, RRH, WA Herb]. Where unvouchered, cannot determine which taxon was recorded	berry salbush
Chenopodiaceae	*Sarcocornia blackiana*	X		y	y	y	1956-99	[*Sarcocornia* sp - RRH, WA Herb]	samphire
Chenopodiaceae	*Sarcocornia quinqueflora*	y	y		y	y	1979-99	[*Salicornia australis* - Storr. *Salicornia quinqueflora* - O'Connor, *Sarcocornia* sp - RRH, WA Herb]	beaded samphire
Chenopodiaceae	*Suaeda australis*	y	y		y	y	1981-99		seablite
Chenopodiaceae	*Threlkeldia diffusa*	y	y	y	y	y	1998-99		coast bonefruit
Colchicaceae	*Wurmbea monantha*	y	y		y		1920s	[*Anguillaria dioica* - Storr. *W. dioica* - O'Connor, Frewer]. One collection about 1920s. Presumed extinct	
Convolvulaceae	*Dichondra repens*	y	y	y	y	y	1956-98		kidney weed
Convolvulaceae	*Wilsonia humilis*	y	y		y	y	1947-1999	[*W. backhousei* - Frewer]	silky wilsonia
Crassulaceae	*Crassula colorata* var. *colorata*	y	y	y	y	y	1956-1999	[*C. colorata* - Storr, O'Connor, M&A, Frewer, WA Herb]	dense stonecrop
Crassulaceae	*Crassula decumbens* var *decumbens*	y	y		y	y	1999	[*C. macrantha* - Storr, O'Connor, *C. decumbens* - Frewer]	rufous stonecrop
Crassulaceae	**Crassula glomerata*					y	1971-99		
Crassulaceae	**Crassula natans* var. *minus*	y	y		y		1956	[*Crassula natans* - Storr, O'Connor, Frewer]. Presumed extinct	
Crassulaceae	**Crassula thunbergiana* subsp *thunbergiana*					y	1999		
Cupressaceae	*Callitris preissii*	y	y	y	y	y	1998-99		Rottnest Island pine
Cymodocaceae	*Amphibolis antarctica*	y			y	y		[*Cymodocea antarctica* - Storr]	seagrass, sea nymph
Cymodocaceae	*Amphibolis griffithii*	X				y			seagrass
Cymodocaceae	*Syringodium isoetifolium*	X				y			seagrass
Cymodocaceae	*Thalassodendron pachyrhizum*	X				y			seagrass
Cyperaceae.	*Carex preissii*	y	y	y	y	y	2000		sedge
Cyperaceae.	*Gahnia trifida*	y	y		y	y	1954-98		coast saw sedge
Cyperaceae.	**Isolepis marginata*	y	y	y	y	y	1998-99	[*Scirpus antarcticus* - Storr, O'Connor. *S. marginatus* - Frewer]	coarse club rush
Cyperaceae.	*Ficinia nodosa*	y	y	y	y	y	1999	[*Scirpus nodosus* - Storr, O'Connor, M&A, Frewer. *Isolepis nodosa* - RRH, WA Herb]	knotted club rush
Cyperaceae.	*Lepidosperma gladiatum*	y	y	y	y	y	1956-98		coastal sword sedge
Cyperaceae.	*Lepidosperma pubisquameum*	y	y	y	y	y	1956-99	[*L. resinosum* - Storr, O'Connor. *L. squamatum* - WA Herb. *L. angustatum* - Storr, O'Connor, M&A, Frewer. L. sp - WA Herb]. See taxonomic issues - appendix 1	
Cyperaceae.	*Schoenus nitens*					y	1999	One collection only, 1999	shiny bog rush
Cyperaceae.	*Baumea juncea*	y	y		y	y	1956-98	[*Hypolaena* sp - Storr, O'Connor, Frewer]	bare twig rush
Dasypogonaceae	*Acanthocarpus preissii*	y	y	y	y	y	1998-99		prickle lily
Droseraceae	*Drosera ramellosa*	X			y	X	1839	Collected Preiss 1839. Recorded A. Weston about 1983 and G. Keighery 1995 near Bickley Swamp	branched sundew
Epacridaceae	*Acrotriche cordata*	y	y	y	y	y	1999-2000		coast ground berry
Epacridaceae	*Leucopogon insularis*	y	y	y	y	y	1956-99	Type collection of this species made at Rottnest	
Epacridaceae	*Leucopogon parviflorus*	y	y	y	y	y	1920s-1999		coast beard-heath

Euphorbiaceae	*Beyeria viscosa*	y	y	y	y	y	1951-99	Recorded Storr 1959, not Storr 1962	pinkwood
Euphorbiaceae	**Euphorbia paralias*					y	1996-1999	Eradication target	sea spurge
Euphorbiaceae	**Euphorbia peplus*	y	y	y	y	y	1995-98		petty spurge
Euphorbiaceae	*Phyllanthus calycinus*	y	y	y	y	y	1920s-2000		false boronia
Euphorbiaceae	*Poranthera drummondii*	y	y	y	y		1920s-1956	[*P. microphylla* - Storr, O'Connor, M&A, Frewer]. Presumed extinct	small poranthera
Euphorbiaceae	**Ricinus communis*	X		y	y	y	1986-98	Cultivated 1884 (Ferguson, 1986). First collected 1986. Eradication target	castor oil plant
Frankeniaceae	*Frankenia pauciflora*	y	y	y	y	y	1998		common sea heath
Gentianaceae	**Centaurium pulchellum*	?X	?		?		1956	See taxonomic issues - appendix 1	
Gentianaceae	*Centaurium spicatum*					y	1998		spike centaury
Gentianaceae	**Centaurium tenuiflorum*	?	?		?	y	1998	See taxonomic issues - appendix 1	
Geraniaceae	**Erodium cicutarium*	y	y	y	y	y	1999		common storksbill
Geraniaceae	**Geranium molle*	y	y	y	y			Presumed extinct in 1998-2001, but collected again in 2002	dove's foot crane's bill
Geraniaceae	*Pelargonium littorale* subsp *littorale*	y	y	y	y		1956	[*P. australe* - Storr, O'Connor. *P. capitatum* - M&A, Frewer]. Only collected 1956, presumed extinct	
Goodeniaceae	*Scaevola crassifolia*	y	y	y	y	y	1920s-99		fan flower
Haemodoraceae	*Conostylis candicans* subsp *calcicola*	y	y	y	y	y	1896-1998	[*C. candicans* - Storr, O'Connor, M&A, Frewer, WA Herb]	grey cottonhead
Hydrocharitaceae	*Halophila ovalis*	X				y			sea wrack, paddle weed
Hydrocharitaceae	*Hydrilla verticillata*	y	y		y		1957	[*Elodea canadensis* - Storr, O'Connor]. Collected 1957 only. Possibly eradicated due to mistaken identification as noxious weed	water thyme
Iridaceae	**Ferraria crispa* subsp. *crispa*	y	y		y	y	1987-99	[*F. undulata* - Storr, O'Connor. *F. crispa* - Frewer.]	black flag
Iridaceae	**Iris* sp					y		Naturalised from cultivated specimens	flag iris
Iridaceae	**Moraea flaccida*					y	1994-99	First collected 1994	one-leaf Cape tulip
Iridaceae	**Moraea miniata*	y	y	y	y	y	1999	[*Homeria miniata* - Storr, O'Connor, M&A, Frewer]	two-leaf Cape tulip
Iridaceae	**Romulea rosea* var. *australis*					y	1999		Guildford grass
Juncaceae	**Juncus bufonius*	y	y		y			Presumed extinct	toad rush
Juncaceae	*Juncus kraussii* subsp *australiensis*	y	y	y	y		1956	[*Juncus maritimus* - Storr, O'Connor. *J. pallidus* - M&A. *J. kraussii* - Frewer]. Collected only 1956. Presumed extinct	shore rush, sea rush
Juncaginaceae	*Triglochin mucronata*	y	y		y	y	1956-99	[*Cycnogeton procerum* - Storr, O'Connor. *Triglochin procera* - Frewer]	prickly arrowgrass
Juncaginaceae	*Triglochin trichophora*	y	y	y	y	y	1956-99	[*T. centrocarpum* var *brevicarpa* - Storr, O'Connor. *T. centrocarpum* - Frewer]	
Lamiaceae	*Westringia dampieri*	y	y	y	y	y	1920s-1998	[*W. rigida* - O'Connor]	westringia
Lobeliaceae	*Lobelia alata*	X				y	1929,'98,'99		angled lobelia
Loganiaceae	*Phyllangium paradoxum*	y	y		y			[*Mitrasacme paradoxa* - Storr, O'Connor, Frewer}. Possibly extinct	wiry mitrewort
Loranthaceae	*Amyema melaleucae*				y			Only collected 1839. Presumed extinct	mistletoe
Malvaceae	*Malva australiana*	y	y		y		1956	[*Lavatera plebeia* - Storr, O'Connor, Frewer]. Offshore islets only Presumed extinct	Australian hollyhock
Malvaceae	**Malva dendromorpha*					y	1994-99	Only from offshore islets and Little Is. in L. Bagdad	European tree mallow
Malvaceae	**Malva parviflora*	y	y		y			Presumed extinct	marshmallow
Meliaceae	**Melia azedarach*				y	y	1999	Naturalised from cultivated specimens	Cape lilac
Mimosaceae	*Acacia cyclops*	y	y	y	y	y	1998	[*A. cyclopis* - Storr, O'Connor]	coastal wattle
Mimosaceae	*Acacia littorea*	y	y		y	y	1839 -1999	[*A. cuneata* - Storr, O'Connor]	
Mimosaceae	*Acacia rostellifera*	y	y	y	y	y	1839-1999		summer-scented wattle
Mimosaceae	*Acacia truncata*						1839	Collected L. Preiss 1839. Presumed extinct	
Moraceae	**Ficus rubiginosa*					y		Naturalised from cultivated specimens	
Myoporaceae	*Eremophila glabra* subsp *albicans* ms	y	y	y	y	y	1903-98	[*E. glabra* - Storr, O'Connor, M&A, Frewer, RRH, WA Herb]	tar bush
Myoporaceae	*Myoporum caprarioides*	y	y		y	y	1999	[*M. viscosum* - Storr, O'Connor]	slender myoporum

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	NOTES	COMMON NAME
Myoporaceae	*Myoporum insulare*	y	y	y	y	y	1945-99	[*M. adscendens* - M&A. *M. tetrandrum* - WA Herb]	boobialla, blueberry tree
Myrtaceae	**Eucalyptus utilis*				y	y		[*E. platypus* var. *heterophylla* - Frewer]. Naturalised	coastal moort
Myrtaceae	*Melaleuca lanceolata*	y	y	y	y	y	1921-99	[*M. pubescens* - Storr]	Rottnest Island teatree
Orchidaceae	*Caladenia latifolia*	y	y	y	y	y	1928-99		pink fairies
Orchidaceae	*Cyrtostylis huegelii*	y	y	y	y	y	1999	[*Acianthus reniformis* - Storr, O'Connor, M&A, Frewer]	midge orchid
Orchidaceae	*Eriochilus dilatatus*	y	y		y	X			white bunny orchid
Orchidaceae	*Leporella fimbriata*	X				X		Recorded on Rottnest, pers. comm. A. Brown	hare orchid
Orchidaceae	*Microtis media*	X				X		Recorded on Rottnest, pers. comm. A. Brown	mignonette orchid
Orchidaceae	*Prasophyllum giganteum*	y	y		y	X	1920s	[*Prasophyllum* sp - Storr, O'Connor, Frewer]	bronze leek porchid
Orchidaceae	*Pterostylis aspera*	X				X		Recorded for Rottnest, pers. comm A. Brown	brown-veined shell orchid
Orchidaceae	*Pterostylis sanguinea*	X				X		Recorded for Rottnest, pers. comm A. Brown	dark banded greenhood orchid
Orobanchaceae	**Orobanche minor*	y	y	y	y			[*Orobanche australiana* - Storr, O'Connor, M&A]. Presumed extinct	lesser broomrape
Oxalidaceae	**Oxalis corniculata*	y	y	y	y	y	1999		yellow wood sorrel
Oxalidaceae	**Oxalis pes-caprae*					X	1990	One collection 1990	soursob
Papillionaceae	**Medicago polymorpha*	y	y	y	y			[*M. denticulata* - Storr, O'Connor]. Presumed extinct	burr medic
Papillionaceae	**Melilotus indicus*	y	y	y	y	y	1999		King Island melilot
Papillionaceae	*Templetonia retusa*	y	y		y	y	1920s-98		cockies' tongues
Papillionaceae	**Trifolium suffocatum*	y	y		y			Presumed extinct	suffocated clover
Papillionaceae	**Trifolium tomentosum*	y	y		y	y	1999		woolly clover
Pittosporaceae	*Pittosporum ligustrifolium*	y	y	y	y	y	1920-99	[*Pittosporum phylliraeoides* - Storr, O'Connor, M&A, Frewer, WA Herb. *Pittosporum phylliraeoides* var. *phylliraeoides* - RRH, WA Herb. *Pittosporum* sp - WA Herb]	
Plantaginaceae	*Plantago debilis*	y	y		y	y	1956-2000	[*P. varia* - Storr, O'Connor. *P. lanceolata* - Frewer]	
Poaceae	**Aira cupaniana*	y	y	y	y	y	1998	[*A. caryophylla* - Storr, O'Connor]	silvery hairgrass
Poaceae	*Austrodanthonia occidentalis*	y	y		y	y	1956-99	[*Danthonia caespitosa* - Storr, O'Connor, Frewer]	
Poaceae	*Austrostipa elegantissima*					y	1998	First collected 1998	feather speargrass
Poaceae	*Austrostipa flavescens*	y	y	y	y	y	1950-1999	[*Stipa variabilis* - Storr, O'Connor. *Stipa flavescens* - M&A, Frewer]	tussock grass
Poaceae	**Avellinia michelii*					X	1995	One collection 1995	
Poaceae	**Avena barbata*	y	y	y	y	y	1998-99	[*A. fatua* - Storr, O'Connor]	bearded oat, wild oat
Poaceae	**Brachypodium distachyon*	y	y			y	1999		false brome
Poaceae	**Briza minor*	y	y		y	y	1999		shivery grass
Poaceae	*Bromus arenarius*	y	y	y	y	y	1956-99		sand brome
Poaceae	**Bromus diandrus*	y	y	y	y	y	1998	[*B. gussonii* - Storr, O'Connor]	great brome
Poaceae	**Bromus hordeaceus*	y	y			y	1998-99	[*B. molliformis* - Storr, O'Connor]	soft brome
Poaceae	**Bromus madritensis*	X					1956	One collection 1956. Possibly extinct	Madrid brome
Poaceae	**Bromus rubens*	y	y	y	y	y	1999		red brome
Poaceae	**Cynodon dactylon*	y	y	y	y	y	1998		couch
Poaceae	**Desmazeria rigida*	y	y	y	y			[*Catapodium rigidum* - M&A, Frewer]. Presumed extinct	rigid fescue
Poaceae	**Ehrharta brevifolia*	y	y		y			[*E. brevifolia* var *cuspidata* - Storr, O'Connor]. Presumed extinct	annual veldtgrass
Poaceae	**Ehrharta longiflora*	y	y	y	y	y	1999		annual veldtgrass
Poaceae	**Eragrostis curvula*					y	1999	Eradication target	African lovegrass
Poaceae	**Hordeum leporinum*	y	y	y	y	y	1999-2000		barley grass
Poaceae	*Lachnagrostis filiformis*					*y*	*1998*	*Specimen no: E Fox 005 22.11.1998 (Perth 055336333)*	

Poaceae	**Lagurus ovatus*	y	y	y	y	y	1956-99		hare's tail grass
Poaceae	**Lolium rigidum*	y	y	y	y			[*Lolium* sp - M&A]. Presumed extinct	annual ryegrass
Poaceae	**Parapholis incurva*	y	y	y	y	y	1999		coast barbgrass
Poaceae	**Pennisetum clandestinum*	y	y		y			Presumed extinct	kikuyu
Poaceae	**Poa annua*	y	y	y	y	y	1998-2000		winter grass
Poaceae	*Poa poiformis*	y	y	y	y	y	1951-99	[*Poa caespitosa* - Storr, O'Connor]	coastal poa
Poaceae	**Polypogon maritimus*	y	y		y	y	1951-99		coast beardgrass
Poaceae	**Polypogon monspeliensis*	y	y	y	y	y	1998-99		annual beardgrass
Poaceae	*Polypogon tenellus*	X					1956	One collection 1956. Presumed extinct	
Poaceae	**Rostraria cristata*	y	y		y	y	1998-99	[*Koeleria phleoides* - Storr, O'Connor. *Trisetaria cristata* - Frewer]	annual cat's tail
Poaceae	**Sorghum bicolor*						1946-47	Collected 1946-47. Presumed extinct	grain sorghum
Poaceae	*Spinifex hirsutus*	y	y	y	y	y	1999		hairy spinifex
Poaceae	*Spinifex longifolius*	y	y	y	y	y	1998		beach spinifex
Poaceae	*Sporobolus virginicus*	y	y	y	y	y	1998		marine couch
Poaceae	**Stenotaphrum secundatum*	y	y	y	y	y	1986-99		buffalo grass
Poaceae	**Vulpia fasciculata*					y	1998-99	First collected 1998	one-glume fescue
Poaceae	**Vulpia muralis*					y	1999	First collected 1999	silver grass
Poaceae	**Vulpia myuros*	y	y	y	y	y	1997-98		silver grass
Polygalaceae	*Comesperma confertum*	?X	?				1956	[*Comesperma* sp - Storr, O'Connor]. Cannot determine which taxon Storr and O'Connor recorded. Presumed extinct	
Polygalaceae	*Comesperma integerrimum*	?X	?	y	y		1903-56	[*Comesperma* sp - Storr, O'Connor]. Cannot determine which taxon Storr and O'Connor observed. Presumed extinct	
Portulacaceae	*Calandrinia* aff *eremaea*					y	1999	Specimen no: J Dodd 753 18/09/99 (Perth 05565979). Probably an unnamed taxon	twining purslane
Portulacaceae	*Calandrinia brevipedata*	y	y			y	1994-99	[*C. calyptrata* - Storr, O'Connor]	short-stalked purslane
Portulacaceae	*Portulaca oleracea*	y	y					Presumed extinct	purslane
Posidoniaceae	*Posidonia australis*	y	y		y	y			seagrass, fibreball weed
Posidoniaceae	*Posidonia coriacea*	X				y			seagrass
Posidoniaceae	*Posidonia sinuosa*	X				y			seagrass
Potamogetonaceae	*Ruppia polycarpa*	y	y		y	y	1956-99	[*R. maritima* - Storr, O'Connor]	sea tassel
Potamogetonaceae	*Ruppia tuberosa*					X	1980	One collection only, 1980	
Primulaceae	**Anagallis arvensis*	y		y		y	1999	[*A. femina* - Storr]	pimpernel
Primulaceae	**Anagallis arvensis* var *caerulea*		y		y	y	1999	(Authority: Marchant *et al.* 1987)	pimpernel
Primulaceae	*Samolus repens*	y	y	y	y	y	1951-99		creeping brookweed
Ranunculaceae	*Clematis linearifolia*	y	y	y	y	y	1920s-1999	[*C. microphylla* - Storr, O'Connor, M&A, Frewer]	old man's beard, slender clematis
Ranunculaceae	*Ranunculus pumilio* var *politus*	y	y		y	y	1956-99	[*R. parviflorus* - Storr, O'Connor. *R. sessiliflorus* - Frewer]	small flower buttercup
Resedaceae	**Reseda alba*						1920s	Collected about 1928. Presumed extinct	white mignonette
Resedaceae	**Reseda luteola*	y					1951	Collected 1951. Presumed extinct	wild mignonette
Rhamnaceae	**Rhamnus alaternus*					y	1998-99	Eradication target	buckthorn
Rhamnaceae	*Spyridium globulosum*	y	y	y	y	y	1920s-1999		basket flower
Rubiaceae	**Galium murale*	y	y	y	y	y	1946-99		small bedstraw
Rutaceae	*Boronia alata*	y	y	y	y	y	1918-98		winged boronia
Rutaceae	*Diplolaena dampieri*	y	y	y	y	y	1920s-1998		southern diplolaena
Sapindaceae	*Dodonaea aptera*	y	y	y	y		1956	Apparently extinct	coast hopbush
Scrophulariaceae	**Cymbalaria muralis*					y			ivyleaf toadflax
Scrophulariaceae	**Parentucellia latifolia*	y						Presumed extinct	common bartsia

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	NOTES	COMMON NAME
Scrophulariaceae	**Dischisma arenarium*	y	y	y	y	y	1951-99		
Solanaceae	*Anthocercis littorea*					y	1999	First collected 1999	yellow tailflower
Solanaceae	**Lycium ferocissimum*	y	y			y	1996		african boxthorn
Solanaceae	**Lycopersicon esculentum*					y	1999	One specimen in mulch near tip 1999	tomato
Solanaceae	**Nicotiana glauca*	y	y	y		y	1998-99	Eradication target	tree tobacco
Solanaceae	**Solanum nigrum*					y	1998	First collected 1998	black berry nightshade
Solanaceae	*Solanum symonii*	y	y	y	y	y	1918-98	[*Solanum simile* - Storr]	
Stackhousiaceae	*Stackhousia monogyna*	y	y		y	y	1951-99	[*S. pubescens* - Storr (recorded Storr 1959), O'Connor, Frewer]	
Sterculiaceae	*Guichenotia ledifolia*	y	y	y	y	y	1918-99		
Sterculiaceae	*Thomasia cognata*	y	y	y	y	y	1900-99		
Urticaceae	*Parietaria cardiostegia*	y	y	y	y	y	1974-99	[*P. debilis* - Storr, O'Connor, M&A, Frewer, WA Herb]	forest pellitory
Urticaceae	**Urtica urens*	y	y	y	y	y	1986-99		small nettle
Zannichelliaceae	*Lepilaena preissii*	y	y		y	y	1956-2000	[*Althenia preissii* - O'Connor]	slender water mat
Zosteraceae	*Heterozostera tasmanica*	y	y		y	X		[*Zostera muelleri* - Storr, O'Connor. *Zostera mucronata* - Frewer]	eelgrass
Zygophyllaceae.	*Nitraria billardierei*	y	y	y	y	y	1956-99	[*N. schoberi* - Storr, O'Connor]	nitre bush
Zygophyllaceae	*Zygophyllum billardierei*	X					1956	One collection, 1956. Presumed extinct	coast twinleaf
Zygophyllaceae	*Zygophyllum simile*	y	y		y	y	1998-99	[*Z. apiculatum* - Storr, O'Connor, Frewer]	sand twinleaf

APPENDIX 3

DELETED NAMES (see explanatory notes with Appendix 2)

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	CURRENT NAME AND NOTES
Aizoaceae	**Carpobrotus aequilaterus*	y	y					*Carpobrotus virescens*. Misidentification
Aizoaceae	**Cryophytum crystallinum*	y						*Mesembryanthemum crystallinum* (Marchant *et al.* 1987 p78)
Aizoaceae	**Gasoul crystallinum*		y					*Mesembyanthemum crystallinum* (Marchant *et al.* 1987 p78)
Aizoaceae	*Tetragonia amplexicoma*			y			y	*Tetragonia implexicoma*
Aizoaceae	**Tetragonia zeyheri*	y	y					*Tetragonia decumbens* (Paczkowska 2000 p637)
Apiaceae	*Apium australe*	y	y					*Apium annuum*. Probable misidentification, Storr described it as annual
Apiaceae	*Apium prostratum*			y	y			*Apium annuum*. Probable misidentification
Apiaceae	*Didiscus caeruleus*	y						*Trachymene coerulea* (WA Herbarium FloraBase 1998)
Apiaceae	*Didiscus pusillus*	y						*Trachymene pilosa*. See taxonomic issues - appendix 1
Apiaceae	*Hydrocotyle tetragonocarpa*	y	y	y	y		y	*Hydrocotyle hamelinensis*. Probable misidentification
Apiaceae	*Trachymene coerulea*		y	y	y			*Trachymene coerulea* subsp *coerulea*
Asclepiadaceae	**Asclepias fruticosa*	y	y					*Gomphocarpus fruticosus*. (Marchant *et al.* 1987 p 526)
Asphodelaceae	**Anthericum divaricatum*	y						*Trachyandra divaricata* (Marchant *et al.* 1987 p779)
Asphodelaceae	*Bulbinopsis semibarbata*		y					*Bulbine semibarbata* (Marchant *et al.* 1987 p779)
Asteraceae	**Arctotheca nivea*	y						*Arctotheca populifolia* (Marchant *et al.* 1987 p658)
Asteraceae	*Calocephalus brownii*	y	y	y	y			*Leucophyta brownii* (Paczkowska 2000 p604)
Asteraceae	**Carduus tenuiflorus*	y	y		y			*Carduus pycnocephalus*. Probable misidentification
Asteraceae	**Conyza bonariensis*			y				*Conyza albida*. Probable misidentification. *C. albida* the only confirmed *Conyza* on Rottnest
Asteraceae	**Conyza canadensis*				y			*Conyza albida*. Probable misidentification. *C. albida* the only confirmed *Conyza* on Rottnest
Asteraceae	**Erigeron canadensis*	y	y					*Conyza albida*. Probable misidentification. *C. albida* the only confirmed *Conyza* on Rottnest
Asteraceae	**Inula graveolens*	y						*Dittrichia graveolens* (Paczkowska 2000 p621)
Asteraceae	*Millotia tenuifolia*	y	y		y			*Millotia myosotidifolia*. Probable misidentification
Asteraceae	*Podosperma angustifolium*	y						*Podotheca angustifolium* (Green 1985 p272)
Asteraceae	*Senecio lautus*	y		y	y	y	y	*Senecio lautus* subsp *dissectifolius* or *maritimus*. Cannot determine which taxon was recorded
Brassicaceae	**Hymenolobus procumbens*	y	y	y	y			*Hornungia procumbens* (Paczkowska 2000 p621)
Caryophyllaceae	**Cerastium viscosum*	y	y					*Cerastium glomeratum*. (Paczkowska 2000 p606)
Caryophyllaceae	**Arenaria serpyllifolia*	y	y					*Arenaria leptoclados*. Misapplied name (WA Florabase 2003)
Caryophyllaceae	**Sagina apetala*	y	y	y	y			*Sagina maritima*. Probable misidentification
Caryophyllaceae	**Stellaria media*	y	y	y	y	y	y	*Stellaria pallida*. Misidentification
Chenopodiaceae	*Arthrocnemum arbuscula*	y	y					*Halosarcia indica*. See taxonomic issues - appendix 1
Chenopodiaceae	*Arthrocnemum halocnemoides*	y	y					*Halosarcia halocnemoides*. See taxonomic issues - appendix 1
Chenopodiaceae	*Atriplex paludosa*	y	y					*Atriplex cinerea*. Probable misidentification
Chenopodiaceae	*Atriplex* sp						y	
Chenopodiaceae	*Enchylaena tomentosa*	y	y	y	y			*Enchylaena tomentosa* var *tomentosa*
Chenopodiaceae	*Halosarcia halocnemoides*				y			*Halosarcia halocnemoides* subsp *halocnemoides*
Chenopodiaceae	*Rhagodia baccata*	y	y	y	y	y	y	*Rhagodia baccata* subsp baccata and *dioica*
Chenopodiaceae	*Salicornia australis*	y						*Sarcocornia quinqueflora*. (Paczkowska 2000 p632). See taxonomic issues - appendix 1
Chenopodiaceae	*Salicorna quinqueflora*		y					*Sarcocornia quinqueflora* (Marchant *et al.* 1987 p90). See taxonomic issues - appendix 1
Chenopodiaceae	*Sarcocornia* sp.					y	y	Either *Sarcocornia blackiana* or *S. quinqueflora*. Cannot determine which taxon was recorded. See taxonomic issues - appendix 1
Colchicaceae	*Anguillaria dioica*	y						*Wurmbea monantha*. Probable misidentification. (Marchant *et al.* 1987 p788)
Colchicaceae	*Wurmbea dioica*		y		y			*Wurmbea monantha*. Possible misidentification
Convolvulaceae	*Wilsonia backhousei*				y			*Wilsonia humilis*. Possible misidentification
Crassulaceae	*Crassula colorata*	y	y	y	y		y	*Crassula colorata* var *colorata*
Crassulaceae	*Crassula decumbens*				y			*Crassula decumbens* var *decumbens*
Crassulaceae	*Crassula macrantha*	y	y					*Crassula decumbens* (Paczkowska 2000 p608)
Crassulaceae	**Crassula natans*	y	y		y			*Crassula natans* var *minus*
Cymodocaceae	*Cymodocea antarctica*	y						*Amphibolis antarctica* (Marchant *et al.* p730)
Cyperaceae	*Isolepis nodosa*					y	y	*Ficinia nodosa* (WA Herbarium FloraBase)
Cyperaceae	*Lepidosperma angustatum*	y	y	y	y			*Lepidosperma pubisquameum*. See taxonomic issues - appendix 1
Cyperaceae	*Lepidosperma resinosum*	y	y					*Lepidosperma pubisquameum*. See taxonomic issues - appendix 1
Cyperaceae	*Lepidosperma squamatum*						y	*Lepidosperma pubisquameum*. See taxonomic issues - appendix 1

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	CURRENT NAME AND NOTES
Cyperaceae	*Lepidosperma* sp						y	*Lepidosperma pubisquameum*
Cyperaceae	**Scirpus antarcticus*	y	y					*Isolepis marginata* (Paczkowska 2000 p633)
Cyperaceae	**Scirpus marginatus*				y			*Isolepis marginata* (Paczkowska 2000 p633)
Cyperaceae	*Scirpus nodosus*	y	y	y	y			*Ficinia nodosa* (WA Herbarium FloraBase)
Euphorbiaceae	*Poranthera microphylla*	y	y	y	y			*Poranthera drummondii* (Pacskowska p630 *P. drummondii* = *P. microphylla*. However revision in progress by D A Halford for Flora of Australia)
Gentianaceae	**Centaurium erythraea*			y	y		y	*Centaurium pulchellum* or *tenuiflorum*. Probable misidentification. See taxonomic issues - appendix 1
Gentianaceae	**Erythraea centaurium*	y	y					*Centaurium pulchellum* or *tenuiflorum*. Probable misidentification. See taxonomic issues - appendix 1
Geraniaceae	*Pelargonium australe*	y	y					*Pelargonium littorale* subsp *littorale*. Possible misidentification
Geraniaceae	**Pelargonium capitatum*			y	y			*Pelargonium littorale* subsp *littorale*. Possible misidentification
Haemodoraceae	*Conostylis candicans*	y	y	y	y		y	*Conostylis candicans* subsp *calcicola*. Misidentification
Hydrocharitaceae	**Elodea canadensis*	y	y					*Hydrilla verticillata*. Misidentification
Iridaceae	**Ferraria crispa*				y			*Ferraria crispa* subsp *crispa*
Iridaceae	**Ferraria undulata*	y	y					*Ferraria crispa* subsp *crispa* (Paczkowska 2000 p615)
Juncaceae	*Juncus maritimus*	y	y					*Juncus kraussii* subsp *australiensis* (Paczkowska 2000 p622: *J. maritimus* = *J. kraussii*)
Juncaceae	*Juncus kraussii*				y			*Juncus kraussii* subsp *australiensis*
Juncaceae	*Juncus pallidus*			y				*Juncus kraussii* subsp *australiensis*. Possible misidentification
Juncaginaceae	*Cycnogeton procerum*	y	y					*Triglochin mucronata*. Probable misidentification. Marchant 1987 p722: *C procerum* - *Triglochin procera*. Paczkowska p638: - *Triglochin procerum* not found in WA)
Juncaginaceae	*Triglochin centrocarpum*				y			*Triglochin trichophora*. Probable misidentification
Juncaginaceae	*Triglochin centrocarpum* var *brevicarpa*	y	y					*Triglochin trichophora*. Probable misidentification
Juncaginaceae	*Triglochin procera*				y			*Triglochin mucronata*. Probable misidentification. (Paczkowska 2000 p638: *T. procerum* not found in WA)
Lamiaceae	*Westringia rigida*		y					*Westringia dampieri* (Paczkowska 2000 p640)
Loganiaceae	*Mitrasacme paradoxa*	y	y		y			*Phyllangium paradoxum* (Paczkowska 2000 p625)
Iridaceae	**Homeria miniata*	y	y	y	y			*Moraea miniata* (Paczkowska 2000 p621)
Malvaceae	*Lavatera plebeia*	y	y		y			*Malva australiana* (Paczkowska 2000 p622)
Mimosaceae	*Acacia cuneata*	y	y					*Acacia littorea*. Misidentification
Mimosaceae	*Acacia cyclopis*	y	y					*Acacia cyclops*
Myoporaceae	*Myoporum adscendens*			y				*Myoporum insulare* (Paczkowska 2000 p626)
Myoporaceae	*Myoporum tetrandrum*						y	*Myoporum insulare*. Probable misidentification
Myoporaceae	*Myoporum viscosum*	y	y					*Myoporum caprarioides*
Myrtaceae	*Melaleuca pubescens*	y						*Melaleuca lanceolata* (Marchant *et al.* 1987 p415)
Myrtaceae	**Eucalyptus platypus* var *heterophylla*				y			*Eucalyptus utilis* (WA Herbarium FloraBase). Cultivated tree that has naturalised
Orchidaceae	*Acianthus reniformis*	y	y	y	y			*Cyrtostylis huegelii* (Hoffman & Brown 1992, pp225 to 227)
Orchidaceae	*Prasophyllum* sp	y	y		y			*Prasophyllum giganteum*
Orobanchaceae	*Orobanche australiana*	y	y	y				*Orobanche minor*. Misidentification
Papillionaceae	**Medicago denticulata*	y	y					*Medicago polymorpha* (Paczkowska 2000 p624)
Pittosporaceae	*Pittosporum phylliraeoides*	y	y	y	y		y	*Pittosporum ligustrifolium* (Cayzer *et al.* 2000)
Pittosporaceae	*Pittosporum phylliraeoides* var *phylliraeoides*					y	y	*Pittosporum ligustrifolium* (Cayzer *et al.* 2000)
Pittosporaceae	*Pittosporum* sp						y	*Pittosporum ligustrifolium*
Plantaginaceae	**Plantago lanceolata*				y			*Plantago debilis*. Probable misidentification
Plantaginaceae	**Plantago varia*	y	y					*Plantago debilis*. Probable misidentification. (Paczkowska 2000 p629: *P. varia* has not occurred in WA)
Poaceae	**Koeleria phleoides*	y	y					*Rostraria cristata* (Paczkowska p622: *K. phleoides* - *Trisetaria cristata*, which is *Rostraria cristata* Paczkowska p638)
Poaceae	**Aira caryophyllea*	y	y					*Aira cupaniana*. Probable misidentification
Poaceae	**Avena fatua*	y	y					*Avena barbata*. Possible misidentification
Poaceae	**Bromus gussonii*	y	y					*Bromus diandrus* (Paczkowska 2000 p603)
Poaceae	**Bromus molliformis*	y	y					*Bromus hordeaceus* (Paczowskza 2000 p603)
Poaceae	**Catapodium rigidum*			y	y			*Desmazeria rigida* (WA Herbarium FloraBase)
Poaceae	*Danthonia caespitosa*	y	y		y			*Austrodanthonia occidentalis*. Probable misidentification
Poaceae	**Ehrharta brevifolia* var *cuspidata*	y	y					*Ehrharta brevifolia*
Poaceae	**Lolium* sp			y				*Lolium rigidum*
Poaceae	*Poa caespitosa*	y	y					*Poa poiformis* (Marchant & Abbott, 1981 p57)
Poaceae	*Stipa flavescens*			y	y			*Austrostipa flavescens* (Paczkowska 2000 p635)

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	CURRENT NAME AND NOTES
Poaceae	*Stipa variabilis*	y	y					*Austrostipa flavescens*. Misidentification (Paczkowska p636: *S. variabilis* = *Austrostipa variabilis*, but this is unlikely to occur on Rottnest)
Poaceae	**Trisetaria cristata*				y			*Rostraria cristata* (Paczkowska 2000 p638)
Polygalaceae	*Comesperma* sp	y	y					Either *Comesperma confertum* or *Comesperma integerrimum*. Cannot determine which taxon was observed
Portulaceae	*Calandrinia calyptrata*	y	y					*Calandrinia brevipedata*. Probable misidentification
Potamogetonaceae	*Ruppia maritima*	y	y					*Ruppia polycarpa*. Misidentification
Primulaceae	**Anagallis femina*	y						*Anagallis arvensis* var *caerulea* (Marchant *et al.* 1987 p196)
Ranunculaceae	*Clematis microphylla*	y	y	y	y			*Clematis linearifolia* (Paczkowska 2000 p607)
Ranunculaceae	*Ranunculus parviflorus*	y	y					*Ranunculus pumilio* var *politus* (Paczkowska 2000 p631)
Ranunculaceae	*Ranunculus sessiliflorus*				y			*Ranunculus pumilio* var *politus*. Probable misidentification
Restionaceae	*Hypolaena* sp	y	y		y			*Baumea juncea*. Probable misidentification
Solanaceae	*Solanum simile*	y						*Solanum symonii*. Misidentification
Stackhousiaceae	*Stackhousia pubescens*	Y	y		y			*Stackhousia monogyna* (Paczkowska 2000 p635). Storr's record: Storr 1959, not 1962
Urticaceae	*Parietaria debilis*	y	y	y	y		y	*Parietaria cardiostegia*. Misidentification
Zannichelliaceae	*Althenia preissii*		y					*Lepilaena preissii* (Marchant *et al.* 1987 p732)
Zosteraceae	*Zostera mucronata*				y			*Heterozostera tasmanica*. Misidentification
Zosteraceae	*Zostera muelleri*	y	y					*Heterozostera tasmanica* . Misidentification
Zygophyllaceae	*Nitraria schoberi*	y	y					*Nitraria billardierei* (Paczkowska 2000 p626)
Zygophyllaceae	*Zygophyllum apiculatum*	y	y		y			*Zygophyllum simile*. Probable misidentification

APPENDIX 4

CULTIVATED SPECIES (see explanatory notes with Appendix 2)

FAMILY	BOTANICAL NAME	1	2	3	4	5	6	NOTES	COMMON NAME
Anacardiaceae	**Schinus terebinthifolius*				y	y			Japanese pepper tree
Araucariaceae	**Araucaria heterophylla*				y	y		Authority: Bodkin 1993	Norfolk Island Pine
Arecaceae	**Phoenix canariensis*				y	y		Authority: Bodkin 1993	Canary Island date palm
Arecaceae	**Phoenix dactylifera*					y			date palm
Arecaceae	**Washingtonia filifera*				y	y			cotton palm
Arecaceae	**Washingtonia robusta*					y		Authority: Bodkin 1993	cotton palm
Bignoniaceae	**Tecoma stans*					y			
Caesalpiniaceae	**Ceratonia siliqua*				y	y		Authority: Bodkin 1993	carob
Casuarinaceae	**Casuarina obesa*				y				swamp sheoak
Casuarinaceae	**Casuarina equisetifolia*					y		Authority: Bodkin 1993	sheoak
Cupressaceae	**Cupressus* sp					y			cypress
Malvaceae	**Lagunaria patersoniana*					y			Norfolk Island hibiscus
Melianthaceae	**Melianthus major*					y	y		honey flower
Moraceae	**Morus alba*					y		Probably *Morus alba*	mulberry
Moraceae	**Ficus carica*		y			y	y		common fig
Moraceae	**Ficus elastica*					y		Authority: Bodkin 1993	rubber tree
Moraceae	**Ficus macrophylla*				y	y		Authority: Bodkin 1993	Moreton Bay Fig
Moraceae	**Ficus microcarpa* var *hillii*					y		Possibly *Ficus microcarpa* var *hillii*	
Myrtaceae	**Agonis flexuosa* var *flexuosa*				y	y		[*A. flexuosa* - Frewer]	peppermint tree
Myrtaceae	**Melaleuca armillaris*					y		Authority: Bodkin 1993	crepe honeymyrtle
Myrtaceae	**Melaleuca huegelii*					y			chenille honeymyrtle
Myrtaceae	**Melaleuca nesophila*					y			mindiyed
Myrtaceae	**Callistemon* sp					y		Probably hybrid	bottlebrush
Myrtaceae	**Eucalyptus camaldulensis*				y	y			river gum
Myrtaceae	**Eucalyptus decipiens*				y				spearwood mallee
Myrtaceae	**Eucalyptus erythrocorys*					y			illyarrie
Myrtaceae	**Eucalyptus gomphocephala*				y	y			tuart
Myrtaceae	**Eucalyptus camaldulensis* var *obtusa*					y			
Myrtaceae	**Eucalyptus spathulata*					y			
Oleaceae	**Olea europaea*				y	y	y		olive
Phormiaceae	**Phormium tenax*					y		Authority: Bodkin 1993	New Zealand flax
Pinaceae	**Pinus halepensis*				y	y			Aleppo pine
Pinaceae	**Pinus radiata*					y			radiata pine
Salicaceae	**Salix* sp					y		Authority: Bodkin 1993	willow
Tamaricaceae	**Tamarix aphylla*					y			tamarisk, athel tree

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Structure and productivity of inland mangrove stands at Lake MacLeod, Western Australia

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Abstract

Lake MacLeod has the largest area of inland mangroves in the world, where communities of stunted *Avicennia marina* (Forsk) Vierh occur isolated from coastal mangroves. These mangroves exist in extremes of environmental stress, mainly related to high salinity, as a consequence of the extreme environment associated with their location on the margins of a non-tidal salt lake in an arid climate. Characteristics of this unique mangrove system are described, showing an annual productivity of 855 g dry wt m^{-2} and an average biomass of 121.3 t ha^{-1}. These are equivalent levels to open coastal mangroves in sub-tropical Eastern Australia. Phenological patterns showed a maximum production of 3–4 g m^{-2} d^{-1} associated with fruiting during late summer, and minimum leaf loss during the winter period June to September.

Keywords: mangroves, *Avicennia marina*, arid, inland, Lake MacLeod, productivity, structure

Introduction

Lake MacLeod is a large saline coastal lake located approximately 30 km north-north-west of Carnarvon, Western Australia. It has an area of 220 000 ha, of which permanent waters cover *ca* 6 000 ha. The salt lake is episodically inundated by fresh water, allowing development of a unique assemblage of wetland types in Australia (Lane *et al.* 1996). These include permanent saline wetlands and inland mangrove swamps that are maintained by subterranean waterways. The lake is a major migration stop-over and drought refuge area for shorebirds, and is also one of the most important non-tidal stop-over sites in Australia. It also supports Australia's and the World's largest inland community of mangroves and associated fauna. Lake MacLeod is listed on the Register of National Estate and is recognised in the Directory of Important Wetlands in Australia (Lane *et al.* 1996).

Lake MacLeod's mangrove community is the larger of only two inland occurrences in mainland Australia; the other is also in Western Australia, at Mandora Salt Marshes (Beard 1967). The Lake MacLeod mangroves occur as low closed-forest to open scrub/shrubland, forming narrow margins that fringe water bodies at the sinkholes, channels and the central lake. Surrounding areas support low open samphire shrubland. There are two main areas, 7.5 ha at North Cygnet Pond, and 15 ha at South Cygnet Pond (Johnstone 1990). The only mangrove species occurring in Lake MacLeod is *Avicennia marina* (Forsk) Vierh, which is the only mangrove species to reach this far south on the WA coast (Semeniuk 1993).

Mangroves inhabit the intertidal zone of sheltered shores in the tropics or sub-tropics. Those that occur inland, isolated from the ocean, are very unusual and for this reason these rare cases are well described in the literature. Because mangrove seeds or propagules are dispersed by seawater, these inland locations are usually relics of a former sea level, so have geological interest.

Several limestone islands in the Caribbean area have inland saline ponds connected with the ocean by submarine caves, supporting inland mangroves. In Bermuda there are many small mangrove areas, some occurring in inland anachaline ponds that exchange water with the ocean through submarine caves (Thomas, 1993). These occur at sea level, and water salinity is around 35 ‰. Thomas *et al.* (1992) described biotic characteristics of the largest mangrove ponds, finding species variability of mangrove and root biota between ponds, caused by isolation of communities. In the Bahamas, mangroves 50 km inland are described from Inagua by Lugo (1981) at three locations with no apparent connection with the ocean. The island is limestone, and the inland mangrove areas are cut off from the ocean by lithified beach ridges. Evaporation from the large shallow lakes raises salinity to up to 70 ‰, which has the effect of stunting the mangrove trees. Barbuda has inland mangrove ponds 2–4 km from the ocean and separated by Pleistocene beach ridges of 2–4 m in height (Stoddart *et al.* 1973). These inland *Rhizophora* thickets are dense and productive, but tended to be of lower height than the 7 m coastal *Rhizophora* on Barbuda. The distribution was interpreted as a geological relic, caused by sea-level change.

In the South Pacific, Woodroffe (1987) described inland mangroves on a small island of Tuvalu, Nanumanga, where mangroves fringe a water body that

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has no connection with the ocean. Here, inland mangroves, mostly *Rhizophora stylosa*, comprise 9.2 % of the island area.

In the Indian Ocean, Van Steenis (1984) described a unique stand of mangroves (*Bruguiera* sp) on the eastern shore terrace of Christmas Island. The stand is 0.33 ha, 120 m inland and occurs between the elevations of 24 to 37 m above sea level (Woodroffe 1988). Corals in growth position on the terrace were dated to the last interglacial, suggesting that this stand of mangroves has persisted as a shoreline relict during the last 120 000 years of lower sea level. The stand occurs at a freshwater spring, where the mean annual rainfall is 2 000 mm. Large *Bruguiera* here indicate that the genus grows well in fresh water, with good regeneration.

In northern Irian Jaya, Van Steenis (1963) described the mangrove *Sonneratia caseolaris* growing at a freshwater lake around 75 m above sea level. This is attributed to the geological uplifting of northern New Guinea. The same species has been observed growing inland at Timika in southern Irian Jaya, close to the Mile 21 replanting station of Freeport mine (J Ellison, University of Tasmania, personal observation). This location is 10 m above sea level, on a riverbank, and about 10 km inland from the estuarine mangroves.

In Western Australia, Beard (1967) described a large mangrove community 25 km inland of the 80 Mile Beach, at Mandora. The location is a salt creek in limestone, which is lined by mangrove trees of up to 5 m (*Avicennia marina*). There is no tidal connection with the ocean at the site.

These examples all indicate that mangroves occurring inland have been cut off from the open ocean by geological enclosure or sea-level change, most commonly on limestone islands. Thus they would have been isolated from the coastal mangrove genetic pool since the cut off time. The characteristics of inland mangroves at Lake MacLeod are investigated here.

The objective of this study was to establish a baseline survey of the mangroves on Lake MacLeod, to characterise these unique mangroves, and to contribute a starting point for long-term monitoring. Monitoring sites were established at three representative areas of the mangrove margins, at the vents, on an island, and in the southern part of Ibis Pond. Measurements were made of stand structure, crown cover, seasonal production and phenology, annual production, growth rates, and plot biomass.

Methods

Lake MacLeod

Lake MacLeod is situated in the Carnarvon Basin at 23° 36'–24° 38' S, 113° 30'–113° 55' E (Fig 1), and is composed of calcareous marine deposits. It is a former sea embayment that was separated from the sea at the south end by development of sand dunes and mid-Holocene sea-level fall. There are few data on the past sea-level patterns from the region, although a mid-Holocene highstand has been modelled, reaching a maximum of 2 m above present sea level at Exmouth Gulf around 6 000 years BP (Lambeck & Nakada 1990). To the west of the lake is the Tertiary limestone Quobba Ridge, forming high sea cliffs in places, overlain with sand.

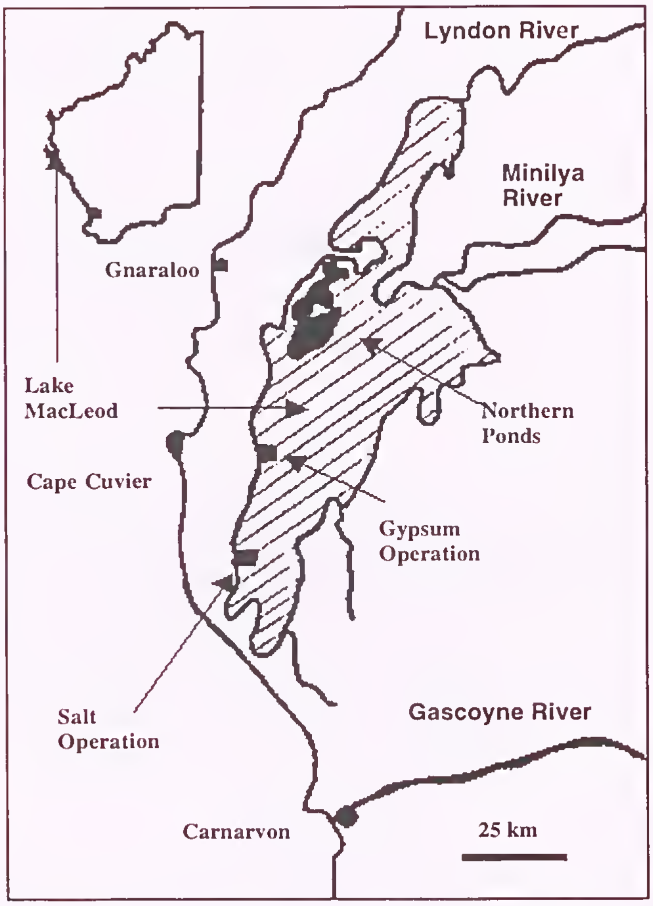

Figure 1. Location of Lake MacLeod and the Northern Ponds.

Ocean water passes underground 18 km through the limestone barrier, driven by a hydraulic head of 3–4 m to rise in sinkholes ("vents") in the central west part of the lake bed (Handforth *et al.* 1984). The lake surface is at an elevation of 3–4 m below sea level, and consists of Cygnet (north) and Ibis (south) Ponds (Fig. 1). The sinkholes, outflow channels and ponds are permanent, although the southern lake varies in area depending on factors such as rainfall or prevailing winds. The vents are several meters in depth; the central pond is *ca* 1 m deep, and the southern pond *ca* 1.5 m deep. The salinity at the vents is close to seawater, with a salinity gradient rising towards the southern pond.

Freshwater enters Lake MacLeod from several creeks and rivers. Surface inflow from Lyndon and Minilya Rivers is episodic (substantial discharge) or near-seasonal (only the nearby lake-bed inundated). Flooding from the Gascoyne River is infrequent, probably once in ten years, but it can cause the lake to be extensively inundated (such as 1989) or to fill (such as 1980 and 2000). However, the climate is arid. Median and mean annual rainfall at Gnaraloo (see Fig 1) are 203 mm and 230 mm respectively, mostly falling in May–July, and annual evaporation across the site is *ca* 2800–3000 mm (Lane *et al.* 1986).

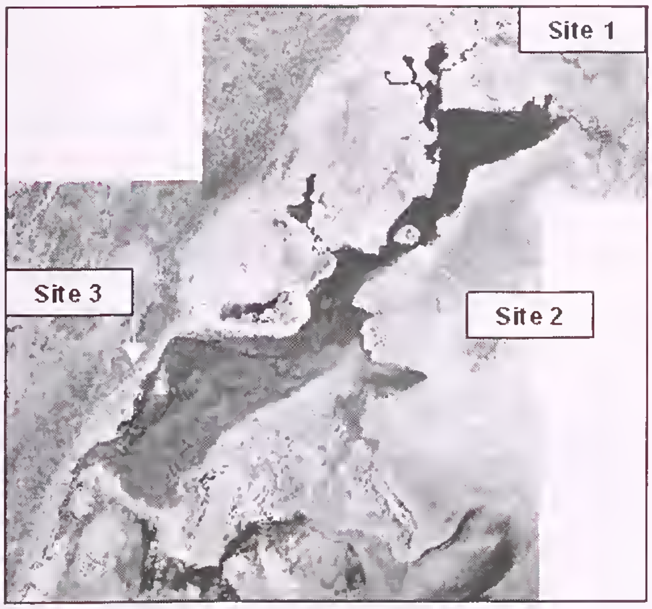

Figure 2. Aerial photograph of Cygnet Pond showing the locations of the three mangrove monitoring sites. Photo 5142 of Minilya (SF49-16) 16/06/95, Western Australian Department of Land Administration.

Monitoring Sites

Permanent plots for monitoring of mangrove community structure were established in December 1997 at three representative sites within the Lake MacLeod mangrove system. The sites (Fig 2) encompass the variability of mangrove types found at Lake MacLeod, of fringing mangroves close to the vents (site 1), on a mid-lake island (site 2), and fringing the main water body at distance from the vents (site 3).

Three replicate permanent monitoring plots, each of 10 x 10 meters, were established at each site location. All trees and seedlings within the plots were tagged and girth measured. Where trees had multiple branches, which occurred in the majority, all were tagged and measured.

Litter fall was measured to quantify vegetative production and phenology. In each plot at each site, two 1 m^2 litter catchers were hung below the mangrove canopy (Saenger & Snedaker 1993). These were emptied each quarter, and the catch oven dried at 60 °C for 2 days, then sorted and weighed. Given the aridity of the Lake MacLeod site, it was possible to empty the litter traps at periods longer than monthly (which was not feasible owing to remoteness and poor access). Trees were re-measured annually, and crown cover and crown density were also estimated in November 1999 to give percent foliage cover (Daubenmire 1959).

Mean tree density and tree height were calculated for each site from the three replicates at each site. Leaf litter data were averaged for the 6 litter catchers at each site, and expressed in dry weight (g) per day for each collection period. Annual variation in production and phenology were analysed from the period September 1998 to September 1999, when collections were most regular.

Biomass was calculated using the allometric relationships established by Clough *et al.* (1997) between stem diameter and above-ground biomass, for the multi-stemmed trees of *Avicennia marina* found in arid northern WA. Their procedure treats each stem as a discrete tree that shares a proportion of the butt and other elements common to all stems. They measured stem diameters of trees located at Port Hedland, Dampier and Exmouth Gulf, at a height of 10–15 cm above the stem junction, then cut the trees and divided them into leaves, branches, stems and butts. From these measurements they determined an allometric equation that estimates tree biomass from stem measurement (Table 2 of Clough *et al.* 1997); $\log(W) = -0.7506 + 2.299 \log(D)$ where W is dry weight (kg) and D is stem diameter (cm). Clough *et al.* (1997) pointed out that it is largely a question of semantics whether or not the multi-branched architecture of arid mangrove trees should be regarded as multi-stemmed or simply multi-branched. The distinction is irrelevant if the allometric relationship is being used to estimate total above-ground biomass or the above-ground biomass of all woody parts of the tree (trunks and branches); it is potentially an issue only if separate estimates of stem biomass and branch biomass are needed.

Results

The mangroves of Lake MacLeod form a narrow margin around permanent ponds, of usually less than 20 m in width, with dense shrub growth. At all sites a distinct zonation in *Avicennia* physiognomy is apparent. The most developed zone is of tall, dense shrubs fringing the water body (Fig 3). The width of this zone is generally 10 m or less, but at Goat Bay (Site 3) the width extended to 50 m in places. The shrub height and zone width of the taller mangroves is greater on shoreline promontories than bays. Adjacent to the Lake MacLeod water bodies, the density of *Avicennia* pneumatophores is far higher than for *Avicennia* on the open coast (Fig 3), indicating low oxygen levels in the soil and interstitial water. This is also a feature of inland mangroves of Bermuda (Thomas 1993), and could be caused by the lack of aeration of mangrove mud without tidal movement.

Behind the shoreline zone is a sharp demarcation from dense mangrove cover to domination by open salt flat,

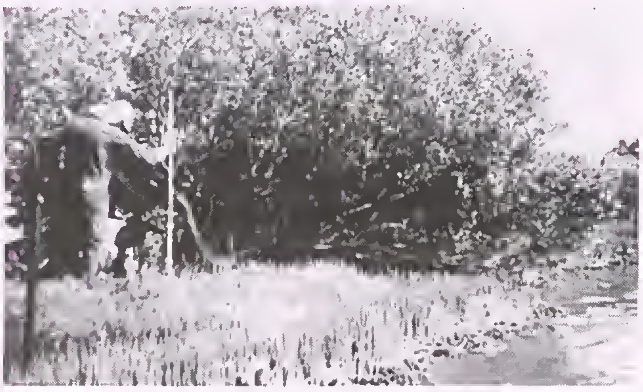

Figure 3. *Avicennia marina* forest fringing Lake MacLeod at site 2, showing multi-stemmed architecture, very dense pneumatophores, and an eroding shore.

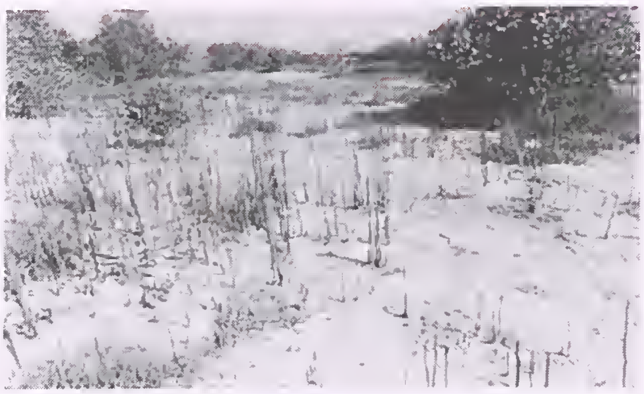

Figure 4. *Avicennia marina* margin with salt flat at Lake MacLeod, showing scattered stunted trees. Also shown is the variability in pneumatophore height at Site 3.

Table 2

Above ground biomass and foliage cover of mangroves at each plot.

Site/ Plot	Biomass (kg 100 m^{-2})	Crown Cover %	Foliage cover %
1A	1186.9	100	70
1B	1221.8	85	51–68
1C	1849.1	95	66.5
2A	1906.1	90	27
2B	927.3	90	45
2C	1004.6	90	36
3A	2548.8	100	80
3B	1039.2	100	70
3C	1215.9	60	42
Mean	**1212.6**	**90**	**55**

with occasional very stunted mangrove shrubs (Fig 4). Samphires (*Halosarcia* sp) occur in both zones. The sharp demarcation between the two zones would be controlled by micro-elevation, and the relatively stable water levels of the ponds.

At site 3 (Goat Bay), mangroves of the zone 2 salt flat margin type had unusual variability in pneumatophore height (*ca* 5–60 cm; Fig 4). This could be due to periods of stationary higher water levels, when the lake floods. In places (*i.e.* adjacent to Plot 1C), *Halosarcia* grows in dense mats over the top of *Avicennia* pneumatophores.

Community structure and biomass

Site descriptions (Table 1) indicate the variable characteristics of these mangrove communities. Biomass of each 100 m^2 plot at Lake MacLeod, using the 1999 stem diameter data and allometric determinations of Clough *et al.* (1997) are given in Table 2.

Site 1 is a taller promontory of older trees, with branches densely overhanging the water. There are no seedlings under the dense canopy. Plot 1C is adjacent to a patch where mangrove trees have recently died. Here *Halosarcia* samphires are densely growing over the *Avicennia* pneumatophores.

Site 2 mangroves occur on a low island central in the pond, where inundation occurs during strong southerly winds. The mangrove margin is narrow, and landward of this (inside the island) is unvegetated salt/mud flats. The exposed nature of site 2 is reflected by the lower heights of trees (Table 1). There is evidence of bank erosion, with horizontal *Avicennia* roots draping over the edge of the bank into open water (Fig 3). Some eroded sediment has been re-deposited among the mangroves within the plots.

At Goat Bay (Site 3), mangroves vary between a narrow margin at plot 3A, to up to a 50 m margin at plot 3C. Plot 3A is largely one multi-stemmed tree, with heavy shading and no samphire growth. Plot 3C has a large amount of dead timber, which pre-dates the monitoring period.

Crown cover

Crown cover values (Table 2) are high, showing that while the mangrove margins are narrow the trees have dense growth. However, foliage cover is particularly low at the island site 2, to give an overall mean of 55%.

Seasonal production and phenology

Averaged production in dry weight g m^{-2} d^{-1} from each site is shown in Figs 5–7, and the total annual production of litter from the Lake MacLeod sites is given in Table 1.

Discussion

Comparing the seasonal productivity and phenology data (Figs 5–7), all sites showed minimum productivity during the winter period of June to September and maximum production during the spring period of August to December. The exception is the high productivity at Site 1 during late summer (March to June). This was caused by heavy fruiting as opposed to leaf production. Phenological patterns are very similar

Table 1

Stand structure data and annual litter production for mangrove monitoring sites at Lake MacLeod.

Site	Tree density m^{-2}	Tree height (m) December 1997	Tree height (m) February 1999	1997–1999 Mortality %	Annual production (g dry wt m^{-2})
1	0.57	3.85	4.05	2.5	1077
2	0.31	2.47	2.46	0	659
3	0.50	2.94	3.10	4.0	829
Mean	**0.46**	**3.09**	**3.20**	**2.1**	**855**

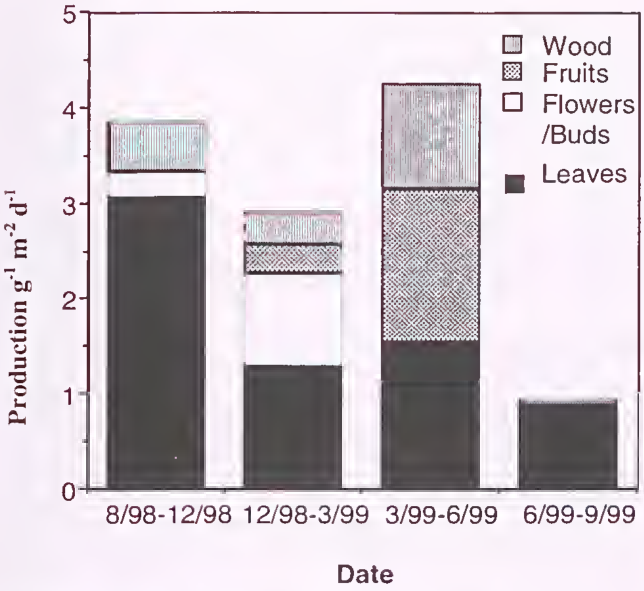

Figure 5. Mangrove litter production, Lake MacLeod site 1.

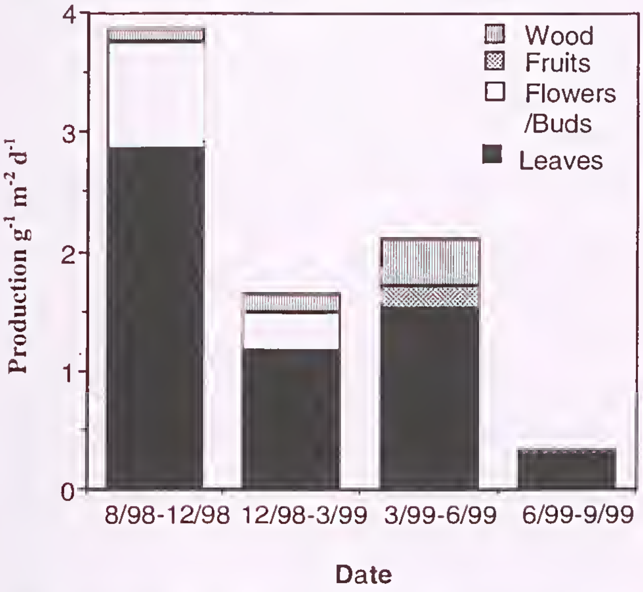

Figure 6. Mangrove litter production, Lake MacLeod site 2.

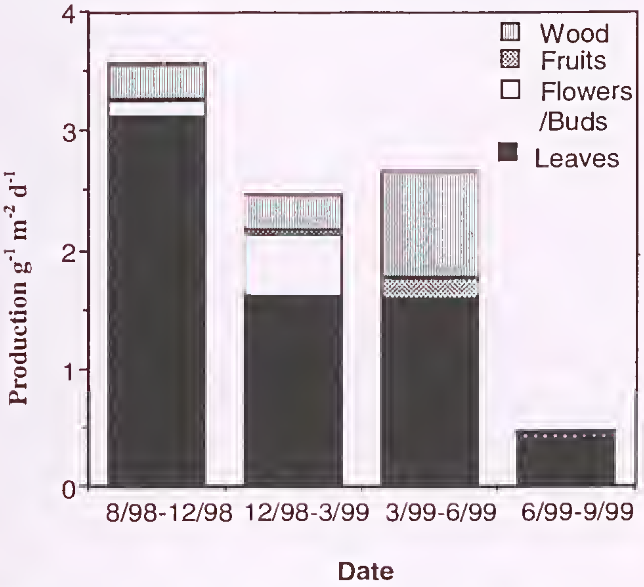

Figure 7. Mangrove litter production, Lake MacLeod site 3.

between sites. Sites 1 and 3 closely correspond, while site 2 differs only in showing slightly later commencement of fruiting. Site 1 showed the highest fruit productivity, which occurred over a longer period, resulting in the highest annual production of sites (Table 1). This may reflect more equable conditions at site 1, being the closest of all sites to the vents, also demonstrated by the taller mean tree heights (Table 1).

Litter productivity over the year is also similar between sites. All sites recorded a maximum leaf production of around 3–4 g m^{-2} d^{-1} in the spring/summer period August to December. The average annual production for MacLeod mangroves of 855 g dry wt m^{-2} is surprisingly high, given the stunted stature of the trees and environmental stresses at the site. However, the mangrove margin is narrow and dense, so this production rate is over a very limited area compared with coastal mangroves. While there are few studies of *Avicennia* productivity in Australia (Saenger & Snedaker, 1993), a similar result was found for a 4 m stand in Queensland by Duke *et al.* (1981). Mackey & Smail (1995) found annual litter fall of subtropical *Avicennia marina* in the Brisbane River, southern Queensland, to be 831–922 g dry wt m^{-2} over two years of measurement. Of this, leaf fall accounted for 47% of the total litter fall, reproductive litter 30%, and woody litter 23%. By comparison, during measurement of the Lake MacLeod mangrove production in the September 1998 to September 1999 period, leaf fall accounted for 68% of the total litter fall, reproductive litter 20%, and woody litter 12%.

This above-ground mangrove biomass from Lake MacLeod *Avicennia marina* (Table 2) is equivalent to 121.3 t ha^{-1}. This result is compared with published above-ground biomass results for *Avicennia marina* of similar height ranges in Australian temperate latitudes (Saenger & Snedaker 1993) in Fig 8. While results are similar, *Avicennia* trees stunted by aridity as opposed to temperature are of heavier biomass, which is to be expected given the butt and multi-branched architecture of these trees (Clough *et al.* 1997).

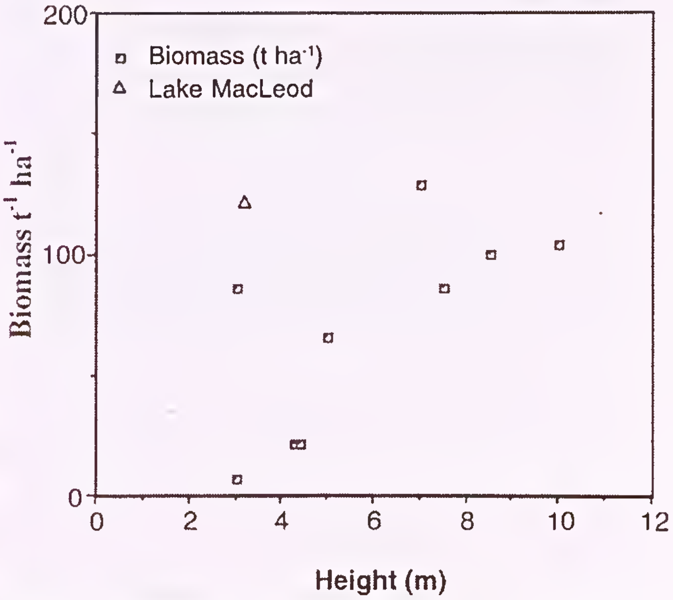

Figure 8. Biomass of *Avicennia marina* at Lake MacLeod compared with *Avicennia* biomass/height records from temperate Australia (data from Saenger & Snedaker, 1993)

Mangrove margins at a number of locations had areas of previous mangrove mortality, although rates over the monitoring period 1997–1999 were 0–4% (Table 1). Adjacent to the vents, there are sections of shoreline where mangrove trees either appear to be unhealthy, with low leaf cover, or the trees are dead. At site 3 (Goat Bay), there is several hundred meters of largely dead mangroves. Occurrence of dead timber in Plot 3C is reflected by the low foliage cover (Table 2). This tree death occurred before December 1997, and may have been caused by storm damage. The broken canopy and relatively large size of trees in this plot may have weakened them to further storm damage. The recorded mortality of 6% in this plot was likely a result of Cyclone Vance in March 1999.

There are several other possible causes of mangrove death at Lake MacLeod. These include salinity stress, as shown at the Embley River estuary in the Gulf of Carpentaria where death of *Avicennia marina* occurred following a series of drier than normal wet seasons, and consequent high soil salinities (Conacher *et al.* 1996). Change in lake water level could also cause mortality, either by increasing salinity stress with a drop in water level, or causing inundation stress with raised water level. Such effects would be documented by continued monitoring at these sites.

In summary, the mangroves of Lake MacLeod are unique, being one of the world's larger inland mangrove areas. Despite their extreme habitat, on the margins of a non-tidal salt lake in an arid climate, these mangroves have high productivity. Rates of primary production, measured by litter fall and mangrove biomass per unit area, are equivalent to mangroves of similar height in normal coastal situations.

The spatial extents of mangroves at Lake MacLeod are obviously controlled by water conditions, particularly water surface elevation that determines the inner margin of mangroves with the salt flat. Water salinity controls mangrove physiognomy, indicated by the stunted architecture of trees more distant from the water's edge. Pneumatophore heights in some areas indicate stress from periods of inundation during higher lake levels, and previous mortality events are apparent from before the period of this study. Having established this baseline study, future monitoring will elucidate these mortality events.

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Groundwater-dependency and water relations of four Myrtaceae shrub species during a prolonged summer drought

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Abstract

Seasonal water relations and water source (δ^2H analysis) data were examined for four Myrtaceae shrub species inhabiting a winter-wet depression (dampland) and surrounding landscape on Perth's coastal sandplain. Data were collected during an exceptionally dry spring-autumn period in 2000/2001. The two species occurring within the dampland, *Astartea fascicularis* and *Pericalymma ellipticum*, were probably accessing shallow soil moisture or groundwater (at a depth of 0.35 m) during October 2000 (spring), but were not accessing groundwater (at a depth of 1.45 m) during the summer drought (March 2001). Species occurring on the dampland embankment (*Hypocalymma angustifolium, Eremaea pauciflora*) and at a site further upslope (*E. pauciflora* only) had a significant reduction in predawn xylem water potential and morning stomatal conductance in response to the summer drought, with neither species accessing groundwater during summer. The dampland species were able to maintain summer morning stomatal conductances similar or greater than the conductance measured during the previous spring, implying that shallow soil moisture (gravimetric content of 10–20%) was sufficient to sustain their summer water-use requirements. δ^2H data suggests that *P. ellipticum* may have been utilising groundwater in early winter (July 2001), implying that the minimum accessible groundwater depth for this species at the study dampland is approximately 1.4 m.

Keywords: dampland, groundwater, sandplain, seasonal water relations, summer drought, winter-wet depression, Myrtaceae

Introduction

Plants occurring above a shallow aquifer may be dependent on groundwater as a regular source of moisture, with the degree of dependency depending on seasonal groundwater and depth, and the species' rooting pattern. Some species only occur where groundwater is at a particular depth, with their loss or decline indicative of an altered hydrological regime caused by a natural decline in water table levels or groundwater extraction (Stromberg *et al.* 1996; Wierda *et al.* 1997). The capacity to exploit an underground water source, or soil moisture at depth, makes it possible for some species to survive long periods without rain (Cramer *et al.* 1999; Williams & Ehleringer 2000).

Perth is on the northern section of a coastal sandplain, under which lies a large, shallow unconfined aquifer (total superficial aquifer groundwater storage of 18 700 x 10^6 m^3; Davidson 1995). This coastal plain consists of urban development, extensive areas of native *Banksia* and other woodlands, introduced pine plantations, and numerous wetlands. Over 50% of the latter have been lost to landfill or drainage (Arnold & Sanders 1981). Shrub species from the family Myrtaceae are a major component of the coastal plain vegetation. The many winter-wet depressions are often dominated by a shrub stratum of shallow-rooted *Astartea fascicularis* (Labill) DC and *Pericalymma ellipticum* (Endl) Schauer. Species such as *Hypocalymma angustifolium* (Endl) Schauer are dominant along the upper edges of these depressions where the soil is rarely waterlogged (Muir 1983; Farrington *et al.* 1990). In more elevated positions deeper-rooted species, *e.g. Eremaea pauciflora* (Endl) Druce, are common.

Populations of myrtaceous shrub species inhabiting low-lying, winter-wet depressions on Perth's sandplains have declined in size since 1966 (Groom *et al.* 2000a). This has been attributed to the gradual decline in groundwater and soil moisture levels in most areas of this aquifer since the 1970s (Heddle 1980; Davidson 1995), resulting from the combined effects of below average rainfall (the sole source of groundwater recharge on the sandplain) and increased regional groundwater abstraction.

Perth experienced its driest spring to autumn period between September 2000 and April 2001 (Bureau of Meteorology, Perth, WA). During this period, the seasonal water relations and groundwater-dependency (by δ^2H analysis) of the abovementioned myrtaceous shrub species were monitored at sites within and adjacent to a winter-wet depression (part of the Lexia wetlands) on the eastern edge of the coastal plain. This study examines how species from different topographical positions within a sandplain landscape sustain their water requirements during periods of drought. It is expected that during times of drought, plants overlying shallow aquifers may rely more on groundwater resources (*i.e.* less on soil moisture reserves) or may be entirely dependent on groundwater. A species' ability to access groundwater during a summer drought may ultimately influence it's distribution within the landscape (Zencich *et al.* 2002).

Materials and Methods

Study site

The Lexia wetlands are a chain of wetlands on the eastern edge of the Gnangara Groundwater Mound, a large, shallow unconfined aquifer on the coastal sandplain north-east of Perth, Western Australia. The Lexia wetlands are unique when compared to other wetlands on Perth's coastal sandplain as they have remained undisturbed from human impact. The majority of the Lexia wetlands are damplands (seasonally waterlogged basins; Semeniuk 1987), which may have surface water depending on the amount of winter rainfall received and regional groundwater levels. A study on the hydrology and stratigraphy of these wetlands indicated that many of the Lexia wetlands may be perched at a soil depth of 2–3 m (Semeniuk & Semeniuk 1993).

The vegetation surrounding these damplands is dominated by an evergreen *Banksia* (Proteaceae)

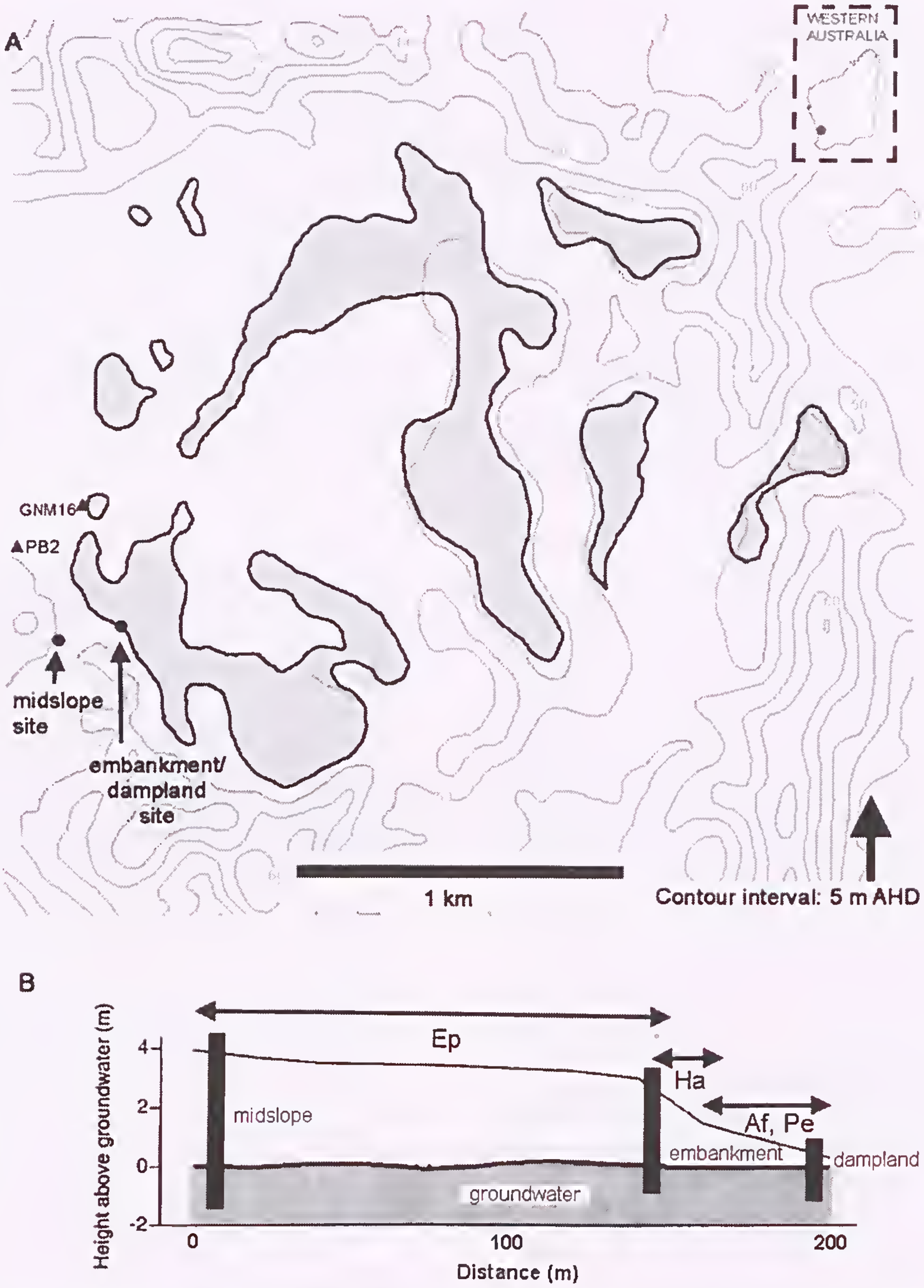

Figure 1. A: Location of study sites and two permanent groundwater monitoring bores (triangles) within the Lexia chain of wetlands (shaded areas), 25 km NE of Perth, Western Australia. B: Distribution of target species and position of sites (thick black lines represent groundwater monitoring piezometers) in the study area. Groundwater profile represents a typical spring (October) water table. Species abbreviations: Af = *Astartea fascicularis*; Pe = *Pericalymma ellipticum*; Ha = *Hypocalymma angustifolium*; Ep = *Eremaea pauciflora*.

overstorey with an understorey of low shrubs from the families Myrtaceae, Proteaceae and Fabaceae (Heddle *et al.* 1980). As groundwater becomes shallower, species tolerant of waterlogging dominate, specifically *Melaleuca preissiana* (Myrtaceae) trees and some myrtaceous shrub species (Farrington *et al.* 1990). Perth's coastal sandplain experiences a dry mediterranean-type climate (Beard 1984) of hot dry summers (December–March) and cool wet winters (June–August), with a long-term average of 870 mm annual rainfall recorded at the Perth meteorological station.

The sites chosen for this study were on the western edge of Lexia wetland number 84 and consisted of dampland, embankment and lower slope sites (Fig 1A). The dampland site (< 1 m depth to groundwater; Fig 1B) at 31°45'23" S 115°57'39" E was dominated by the myrtaceous target species *Astartea fascicularis* and *Pericalymma ellipticum*. The embankment site (2–3 m depth to groundwater) was on the edge of the dampland and had the target species *Hypocalymma angustifolium* (lower section) and *Eremaea pauciflora* (upper section) (Fig 1B). *E. pauciflora* also occurred at the midslope site (3–4 m depth to groundwater) at 31°45'27" S 115°57'26" E, which was located approximately 200 m from the dampland site. Groundwater access tubes were installed at all sites to a depth of approximately 1 m below maximum (spring) groundwater levels.

Seasonal water relations

Water relations of the target species were measured three times during 2000–2001 at dates that reflected seasonal hydrological differences. Data were collected on 31 October 2000 (spring, representing maximum groundwater levels), 19 March 2001 (late summer, representing minimum groundwater levels) and 24 July 2001 (winter, representing the beginning of groundwater recharge). July measurements were taken during the driest start of winter (June–August) that Perth has recorded. Each set of measurements was collected on a cloud-free, sunny day, at least 2 days after the last rainfall event.

Xylem water potentials were measured predawn (0300–0500 h local time; WP_{pd}) and midday (1200–1330 h; WP_{md}) for 3–4 leafy stems per species using a pressure chamber (Model 3005, Soil Moisture Equipment Co., Santa Barbara, CA). Predawn values indicate the maximum water potential, reflecting the degree of overnight recovery of water balance following water deficit incurred during transpiration the previous day. Midday water potential represents the minimum daily value and therefore the maximum stress.

Transpiration and stomatal conductance were measured mid-morning (0930–1030 h) and midday (1230–1330 h) using a portable infra-red gas analyser (LCi, ADC Bioscientific Ltd, Hoddesdon, England) for leaves produced in the previous year of three different plants per species. Afternoon measurements were not conducted as the equipment overheated (and malfunctioned) when the leaf chamber temperature was greater than 35 °C, a common occurrence during the afternoons of spring and summer measurements. Measurements were taken at ambient humidity and CO_2 concentrations, and recorded within 1 min of enclosing the leaf within the chamber. All gas exchange data were collected when light intensity (PAR) was > 1000 µmol m^{-2} s^{-1}. Transpiration and stomatal conductance data were expressed on an area basis, with leaf area measured in the laboratory with a digital image analyser (WinDIAS, Delta-T Devices, Cambridge, UK). Ventilated leaf chambers may alter boundary layer conductance and leaf temperatures (McDermitt 1990) and hence gas exchange parameters. These errors were relatively minor in the context of this investigation because leaves of the study species are small (0.025 – 1.5 cm^2) resulting in a large boundary layer conductance relative to stomatal conductance. Soil-to-leaf hydraulic conductance (K_L), was calculated after Hubbard *et al.* (1999) as midday transpiration/($WP_{pd} - WP_{md}$).

Soil moisture

Soil samples were collected every 0.1 m (dampland) or 0.2 m (other sites) depth and stored in air tight containers. For spring and winter measurements soil samples were collected using a hand-held auger. Augering was not possible for the summer measurement because the soil was too dry. Instead, pits were hand dug until groundwater was reached or augering was possible. Due to safety concerns regarding the stability of the sandy pit walls at the midslope site, soil samples were only collected from the top 2 m of the soil profile. July soil samples were not collected for depths >3 m at the midslope site as winter rainfall had not penetrated below this depth. Soil samples were dried at 100 °C for 24 h and soil moisture was calculated gravimetrically (%) as (fresh weight – dry weight)/dry weight × 100.

Samples for deuterium analysis

Twig samples 5–10 cm in length were collected from three different shrubs per species, and their leaves immediately removed. Twigs were then wrapped in plastic cling wrap to prevent isotopic fractionation by evaporation and placed in an airtight container (see Turner *et al.* 2001). Groundwater samples and data of groundwater depth were collected from groundwater access tubes installed at each site. Soil samples for deuterium analysis were collected at the same time as samples for soil moisture. All samples were stored in airtight containers and kept at ~ 5 °C in the field until transported to the laboratory. Samples were then transferred to a freezer where they remained until the water was extracted. Bark was removed from twig samples prior to water extraction.

Water was extracted from soil and twig samples by cryogenic vacuum distillation (Ehleringer & Osmond 1989). Two Vycor glass tubes were attached to a vacuum pump in a Y-shape configuration. Twig samples or approximately 15 g of soil was placed in one tube and frozen by submerging the tube in liquid nitrogen. Both tubes were evacuated and then isolated from the vacuum line to create a closed U-shape configuration. The tube containing the sample was placed in boiling water, whilst the second tube was placed in liquid nitrogen to 'trap' water evaporating from the heated sample. After 1 h, the collection tube was removed and sealed. After thawing, the collected water was decanted into an airtight vessel.

Extracted water samples and free water samples (groundwater) were reduced to hydrogen gas for analysis using a gas phase mass spectrometer (VG Isogas SIRA 10), and were analysed using the procedure outlined by Coleman *et al.* (1982). Hydrogen/deuterium ratios (δ^2H) were expressed according to standard notation in parts per thousand (‰) relative to the V-SMOW (Vienna Standard Mean Ocean Water) standard as $\delta^2H = ((R_{sample}/R_{standard})-1) \times 1000$, where R_{sample} and $R_{standard}$ are the ratios of the heavy to light isotope of the sample and standard water respectively.

δ^2H was only measured once for all water samples, except for free water samples where duplicate samples were analysed. For soil water δ^2H, soil samples collected at 0.4 m intervals were analysed.

Data analysis

Analyses of variance were calculated using the SuperANOVA (Abacus Concepts, Berkeley, CA) computer package. Homogeneity of variances was checked by residual plots and data were transformed as necessary by log or square roots, with data presented as untransformed means. Tukey's HSD test was used for comparisons between means at the 0.05 significance level.

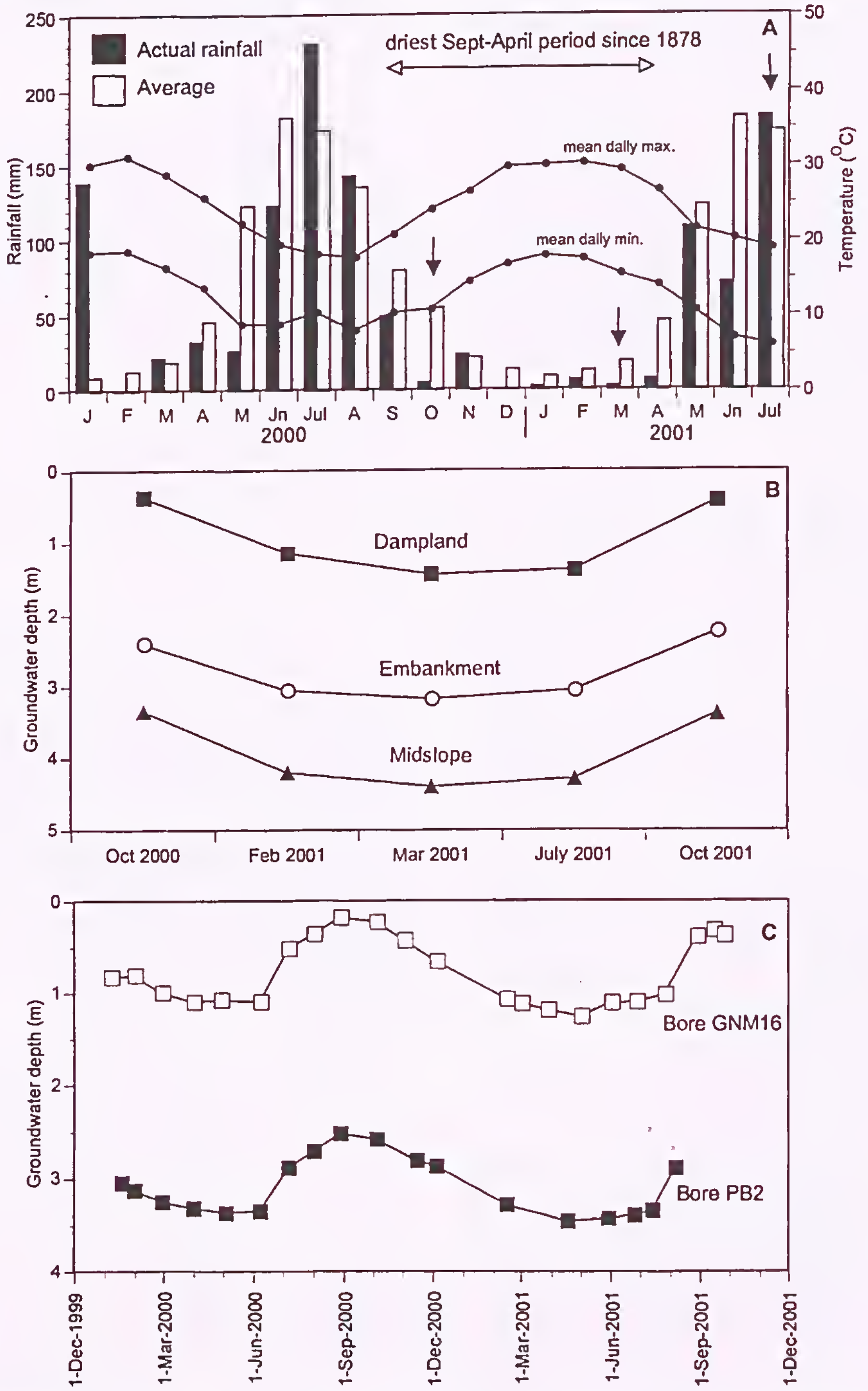

Figure 2. Climate and groundwater data for Perth and Lexia wetlands. A: Rainfall and temperature data for Perth meteorological station from Jan 2000 – July 2001. Arrows represent sampling times for plant water relations; B: groundwater levels *in situ* at the three study sites from Oct 2000 to Oct 2001; C: monthly variation in groundwater levels (Jan 2000 – Sept 2001) from two permanent monitoring bores near the Lexia wetlands (see Fig 1). Bores chosen were those that had similar October 2000 (spring) and March 2001 (summer) groundwater depths to the dampland and midslope study sites.

Results

Climate and groundwater levels

Perth and the surrounding environs (including the Lexia chain of wetlands) experienced an exceptionally dry spring to autumn period (Sept 2000–April 2001) with only 98 mm of rainfall, compared to the long-term average of 258 mm (Fig 2A). In comparison, the previous spring to autumn period was exceptionally wet, with 139 mm of rain recorded in January 2000 (average is 9 mm). Between October 2000 and July 2001 mean daily maximum temperatures peaked during February (30.2 °C) with the lowest maximum temperatures recorded in July (18.8 °C; Fig 2A). Highest (17.4 °C) and lowest (6.0 °C) mean daily minimum temperatures were also recorded in February and July respectively.

At all three topographical positions, groundwater levels were at their lowest by March 2001 and remained so when remeasured in July 2001 (Fig 2B), representing a decrease in groundwater levels ranging from 0.77 m (embankment) to 1.08 m (dampland) compared to October 2000 levels. At permanent monitoring bores situated within close proximity to the study sites (Fig 1A), groundwater levels did not increase until September 2001 (Fig 2C). In 2000 (a year of near-average rainfall) groundwater levels in these bores began to rise in June, as a result of April–May rainfall. By October 2001, groundwater levels at all sites had recovered to October 2000 levels.

Seasonal water relations

There was no significant difference in morning stomatal conductance or transpiration data between species in either spring or winter (Fig 3A, B). Both dampland species (*A. fascicularis* and *P. ellipticum*) had significantly higher ($P < 0.001$) transpiration and stomatal conductance values (transpiration: 1.5–5.3 mmol m^{-2} s^{-1}; conductance: 0.09–0.23 mol m^{-2} s^{-1}) than the other species in summer. *E. pauciflora* at both the embankment and midslope sites had the lowest values of transpiration and stomatal conductance (transpiration: ~0.1 mmol m^{-2} s^{-1}; conductance: < 0.01 mol m^{-2} s^{-1}). *A. fascicularis* transpired at the same rate (~ 2 mmol m^{-2} s^{-1}) and had the same seasonal stomatal conductance (~ 0.1 mol m^{-2} s^{-1}) throughout the study (Fig 3A, B). For *H. angustifolium* and *E. pauciflora* occurring on the embankment and midslope (*E. pauciflora* only) sites, there was a significant decrease in transpiration and stomatal conductance between spring and summer. In *H. angustifolium* there was no significant difference between summer and winter transpiration and stomatal conductance data. Winter stomatal conductance values were similar to those recorded pre-drought in spring for both the embankment and midslope *E. pauciflora*, in contrast to transpiration values (Fig 3B).

Comparison of WP_{pd} data between species for a given season showed that there was no significant differences between the two dampland species or between the embankment and midslope stands of *E. pauciflora*. Spring data varied from −0.09 (*P. ellipticum*) to −0.26 (*H. angustifolium*) MPa (Fig 3C); winter data varied from −0.15 (*H. angustifolium*) to −0.57 MPa (*E. pauciflora*; midslope). *E. pauciflora* had significantly lower ($P=0.0001$) summer WP_{pd} (of around −3.3 MPa) in relation to the other species, with *H. angustifolium* the next lowest WP_{pd} (-1.1 MPa). The two dampland species had summer WP_{pd} > -1 MPa (Fig 3C). Summer WP_{pd} was always significantly more negative than spring and winter data (Fig 3C). There was no significant difference between

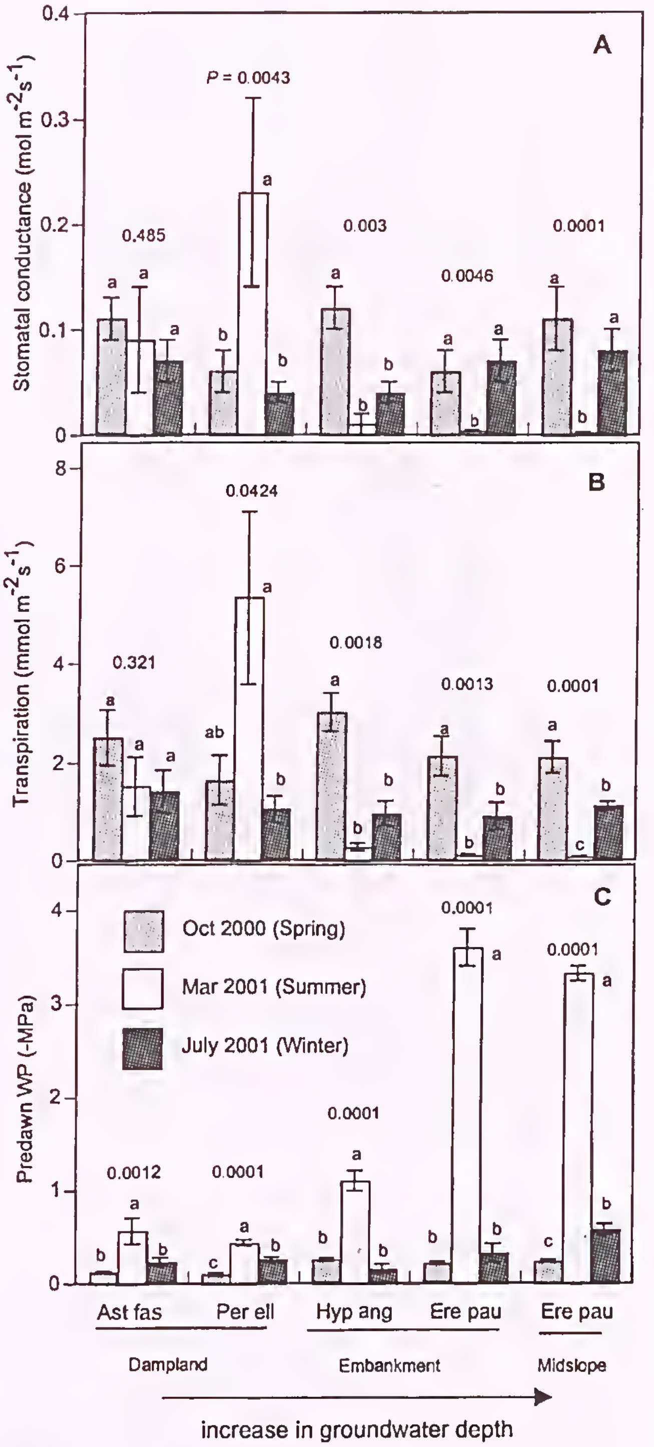

Figure 3. Seasonal water relations patterns. A: morning stomatal conductance, B: morning transpiration and C: predawn xylem water potential, for four myrtaceous shrub species occurring at three positions differing in groundwater depth. Morning data combines mid-morning and midday data (n = 6); predawn data were obtained from 3 individuals per species; values are mean ± se. Probability values are presented from a one-way ANOVA comparing seasonal differences within a species. Similar letters indicate no significant difference between means (Tukey's HSD test, $P<0.05$).

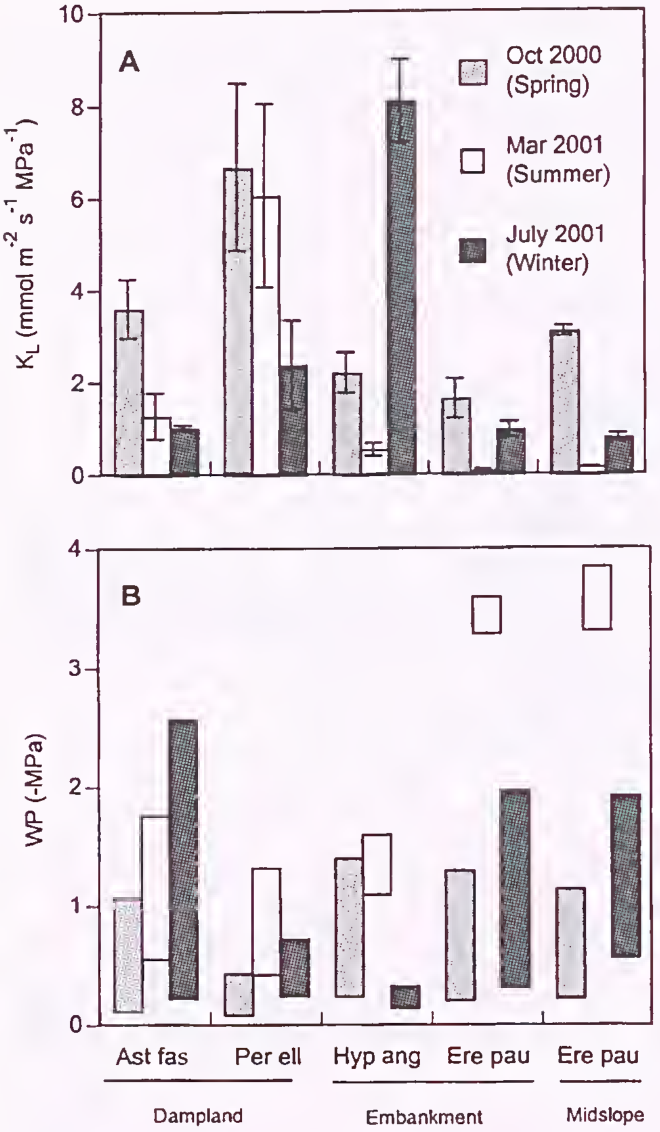

Figure 4. Seasonal water relations patterns for four myrtaceous shrub species occurring at three positions differing in groundwater depth. Values are mean ± se. A: soil-to-leaf hydraulic conductance (K_L). K_L values and se were calculated from the mean and se of transpiration, WP_{pd} and WP_{md} data; B: range of xylem water potential (WP). Lower end of bar is mean WP_{pd}, and the upper end is mean WP_{md}.

winter and spring WP_{pd} data for *A. fascicularis*, *H. angustifolium* and *E. pauciflora* (embankment).

For almost all species, soil-to-leaf hydraulic conductivity (K_L) decreased by 65–95% from spring to summer, except for *P. ellipticum* where K_L remained the same (Fig 4A). Summer K_L was highest for the two dampland species (1.3–6.0 mmol m^{-2} s^{-1} MPa^{-1}) and lowest for both stands of *E. pauciflora* (< 0.2 mmol m^{-2} s^{-1} MPa^{-1}), the latter due to low summer transpiration (Fig 3A) and a relatively small difference (< 0.5 MPa) between WP_{pd} and WP_{md} (Fig 4B). Overall, winter K_L was lower than spring K_L, with the exception of *H. angustifolium*. *H. angustifolium* had the highest winter K_L (8.1 mmol m^{-2} s^{-1} MPa^{-1}), reflecting a relatively large midday transpiration and a difference of only 0.03 MPa between WP_{pd} and WP_{md}.

Soil moisture

Gravimetric soil moisture contents decreased from spring to summer and increased from summer to winter at all sites, with winter data greater than for the previous spring at the embankment and midslope sites (Fig 5). Soil moisture content within the dampland site varied from 8–20% during summer to 20–80% in winter. The soil moisture profiles at the midslope site were the driest of

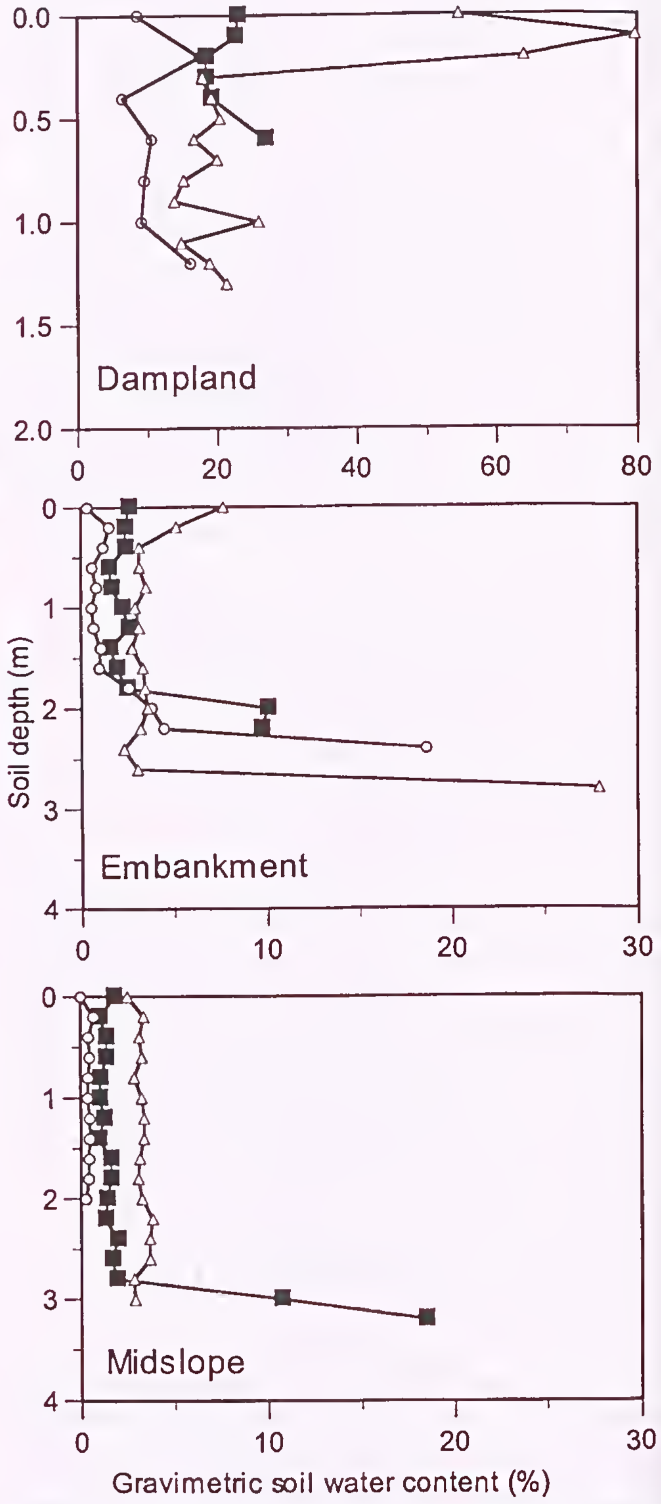

Figure 5. Gravimetric soil moisture profiles at the three topographical locations for spring 2000 (squares), summer 2001 (circles) and winter 2001 (triangles).

all the sites with summer soil moisture content < 0.5% down to 2 m depth (Fig 5). Substantial increases in gravimetric soil moisture contents at depth for the embankment and midslope sites indicate the presence of the capillary fringe, a zone of saturated soil just above the water table.

Deuterium analysis

Groundwater δ^2H was generally less negative than δ^2H in the soil profile (see Fig 6 for exceptions) and became less negative as the seasons progressed, with summer and winter data displaying minimal variation between sites (Fig 7). Dampland spring groundwater δ^2H varied from -16.25 to –21.78 ‰ compared with –16.52 to –19.20 ‰ at the embankment/midslope sites.

For spring and winter data, species with lowest WP_{pd} had the lowest xylem δ^2H (*A. fascicularis* in spring and *H. angustifolium* in winter were the exceptions) (Fig 7). This was not the case in summer, where xylem δ^2H became less negative as WP_{pd} decreased, with the three shallow rooted species (*A. fascicularis, P. ellipticum, H. angustifolium*; all < 1 m rooting depth; Dodd *et al.* 1984) having more negative δ^2H values than *E. pauciflora* (> 2 m rooting depth).

Comparing xylem water δ^2H with soil water and groundwater δ^2H data (Fig 6) it appears that *P. ellipticum* was utilising surface soil moisture (<0.2 m) in spring and soil moisture at relative depth (0.8–1.0 m) in winter. Spring xylem water δ^2H for *A. fascicularis* (-25.29 ± 0.90 ‰; mean ± SD) was less than that of groundwater (-16.25 to -21.78 ‰) and soil moisture (-4.50 to –21.82 ‰). Summer data suggest that both *A. fascicularis* and *P. ellipticum* were accessing soil moisture throughout the profile, although soil water δ^2H at 0.8 m was more negative than the xylem water. Summer xylem water δ^2H of *P. ellipticum* (-29.15 ± 4.62 ‰) was more negative than

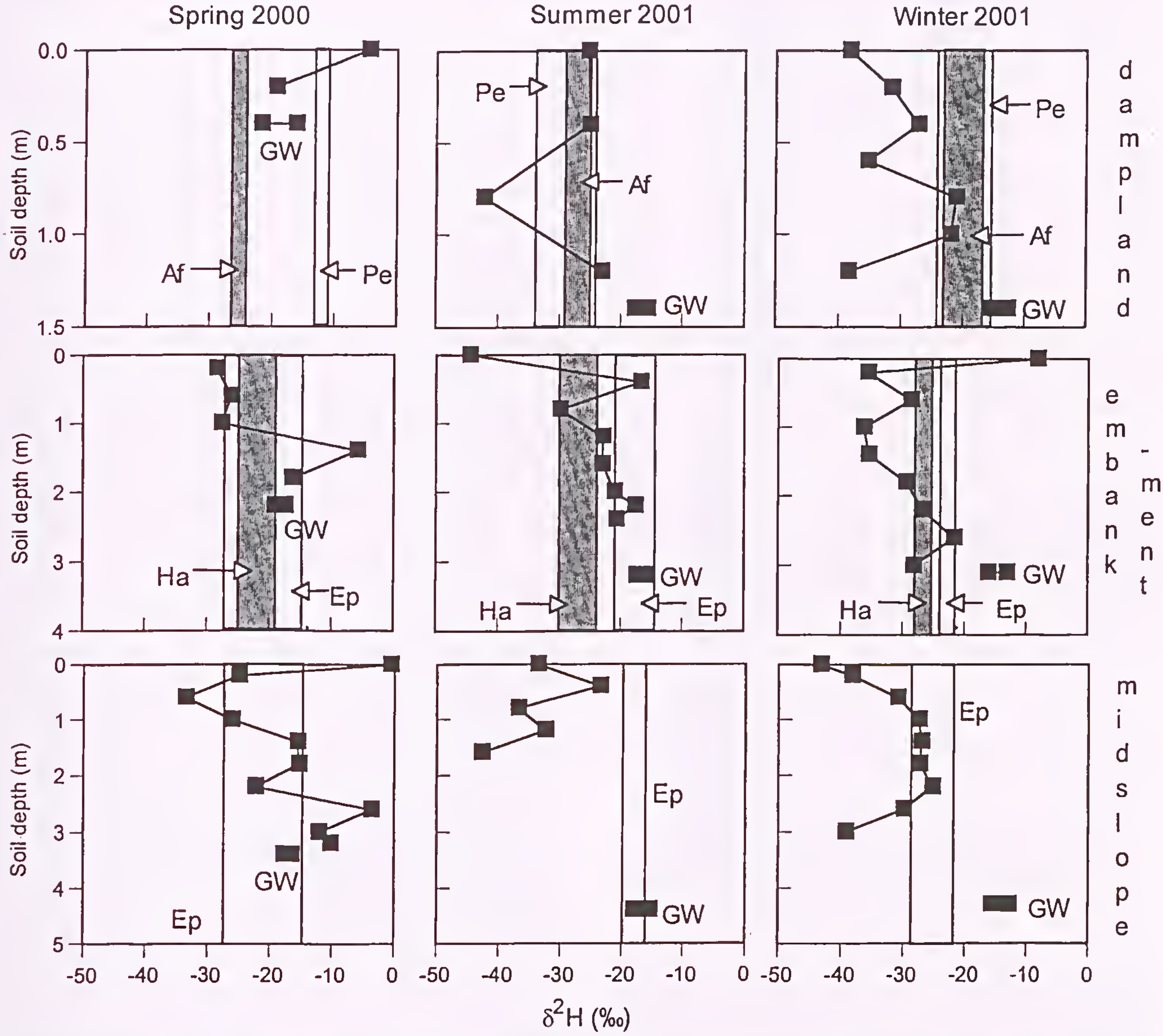

Figure 6. Seasonal profiles of soil δ^2H at the three topographical locations including groundwater (GW) values. Bars represent the range of xylem water δ^2H for the study species at each site. Shaded and unshaded bars are displayed to distinguish between different species at the same site. Summer and winter midslope profiles did not extend below 2 and 3 m respectively. Species abbreviations are provided in Fig 1. The values represent a single analysis from one sample per soil depth.

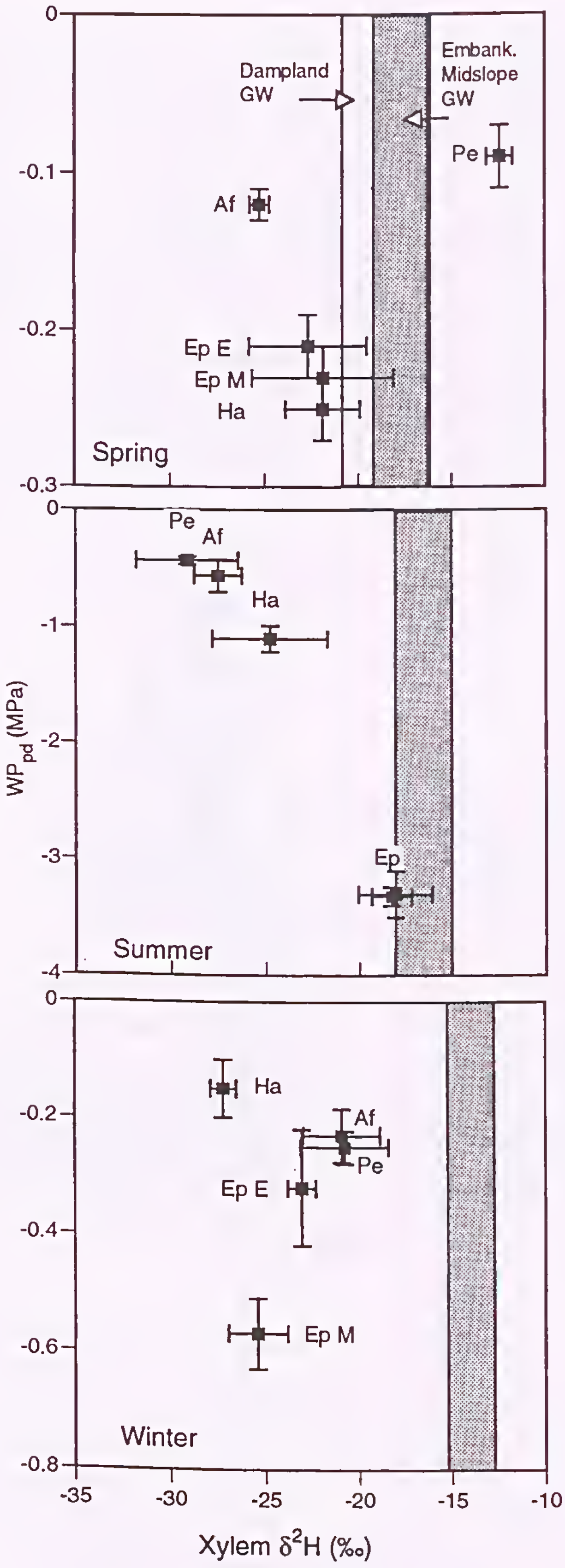

Figure 7. Predawn water potential (WP$_{pd}$) in relation to xylem water δ^{2}H on a seasonal basis. Shaded bars represent the range of groundwater δ^{2}H for the three sites, except for spring data where dampland and embankment/midslope sites are represented by different bars (unshaded and shaded respectively). Species abbreviations are provided in Fig 1. Values are mean ± se for 3 different individuals per species.

that of *A. fascicularis* (-27.54 ± 2.16 ‰). *A. fascicularis* was utilising the same soil moisture source (0.8–1.0 m) as *P. ellipticum* in winter.

At the embankment site, *H. angustifolium* was accessing soil moisture in the top 1 m of the soil profile in spring and summer (Fig 6) and probably in winter. Winter soil water δ^{2}H data coincided with xylem water δ^{2}H at 0.6, 2.2 and 3.0 m; however, *H. angustifolium* was unlikely to be accessing soil moisture at depths > 1 m, due to its shallow-rooted nature (Dodd *et al.* 1984). *E. pauciflora* was accessing moisture from both shallow (< 1 m) and deeper (< 2 m) soil depths in spring and summer at the embankment site, and possibly groundwater. Xylem water δ^{2}H data suggest that *E. pauciflora* was not accessing groundwater when winter data was collected.

It appears that at the midslope site *E. pauciflora* accessed groundwater during spring and summer, but not in winter. *E. pauciflora* was also accessing moisture from depths up to 2 m in the soil profile in summer and between 1–2 m in winter.

Discussion

Summer drought is one of the major environmental factors affecting species survival in south-western Australia (Hnatiuk & Hopkins 1980), with severe or prolonged drought periods considered an extension of the normal summer drought scenario (Hobbs & Mooney 1995). Past studies on plant water relations of Perth's sandplain species have shown that shallow rooted (< 1 m rooting depth) species tend to display more negative water potentials and have substantially lower transpiration rates than co-occurring deeper rooted shrub species during mid-late summer (Grieve 1956; Dodd *et al.* 1984; Dodd & Bell 1993). On the other hand, the present study shows that shallow-rooted species were the least water stressed, compared with the deeper rooted *E. pauciflora* species. The difference between these results is because none of the earlier studies included wetland sites, or sites where summer groundwater depth was < 3 m, whereas all the shallow-rooted species in this study occurred within or fringing a wetland.

The response of myrtaceous shrub species to the extended summer drought of 2000/2001 differed according to their location within the sandplain landscape, as shown by an overall decline in WP$_{pd}$ with increased groundwater depth. A decline in water potential and stomatal conductance was expected during mid-late summer, as species respond to increasing soil moisture deficits. This was the case for *H. angustifolium* and *E. pauciflora* occupying the embankment and midslope sites, and resulted in substantial decreases in soil-leaf hydraulic conductivity, but not for the dampland species. For *H. angustifolium* and *E. pauciflora* the seasonal trends between stomatal conductance and WP$_{pd}$ or hydraulic conductivity suggests a close association between the root/soil system and stomatal response, but does not explain *H. angustifolium*'s relatively large hydraulic conductance in winter. Differences in stomatal responses to soil and atmospheric water deficits between species may be explained by differences in soil-leaf hydraulic conductance and a species threshold water potential (Bond & Kavanagh 1999), the latter being a minimum water potential beyond which the chance of xylem cavitation is greatly increased. Based on the data presented in this paper, it would be expected that the threshold water potential of *E. pauciflora* would be more negative than that of *H. angustifolium*.

The relatively low (approximately -3.3 MPa) WP_{pd} of *E. pauciflora* at the embankment and midslope sites suggests that this species did not have access to groundwater sources by late summer, and is in contrast to the interpretation obtained from comparing xylem δ^2H with that of groundwater and soil water δ^2H data. A lack of discrimination between groundwater δ^2H and soil water δ^2H, as occurred at both *E. pauciflora* sites in spring and the embankment site in summer, makes it difficult to ascertain the main sources of water used (see Burgess *et al.* 2000). In the present study, water potential data suggest that *E. pauciflora* had access to groundwater in October (spring), when groundwater levels were at their highest (2.40 and 3.34 m respectively for the embankment and midslope sites), but did not have access to groundwater in July (mid-winter) when groundwater levels were approximately 0.1 m higher than in March (late summer). It is therefore unlikely that *E. pauciflora* had direct access to groundwater in summer at either site, and this is supported by WP_{pd} data. This suggests that the minimum accessible groundwater depth for *E. pauciflora* at the embankment and midslope sites is between 2.4–3.0 m and 3.4–4.2 m respectively. Based on water potential data, Dodd & Bell (1993) showed that *E. pauciflora* was unable to access groundwater during summer at a depth of 7.2 m, but accessed groundwater during the spring months when the water depth was 6.3 m.

If *E. pauciflora* is not accessing groundwater during the summer period at the embankment site, then it stands to reason that *H. angustifolium* with its shallower root system is also not accessing groundwater. So why is it that *H. angustifolium* had a less negative WP_{pd}? *H. angustifolium* is restricted to and often fringes winter-wet depressions (Marchant *et al.* 1987), and is reliant on shallow soil moisture or groundwater sources when available. Differences in WP_{pd} may be a result of *E. pauciflora* being restricted to the top end of the embankment near where the piezometer was installed (Fig 1), whereas *H. angustifolium* was sampled from the lower edge of the embankment where groundwater levels would have been < 3 m in summer. The negative correlation of summer WP_{pd} with xylem water δ^2H between species (Fig 7) suggests that species reliant on shallow soil moisture sources (< 1 m soil depth) were less water stressed than those utilising deeper soil moisture reserves (*i.e. E. pauciflora*).

Of ten myrtaceous shrub species examined for their long-term (30 years) response to decreasing groundwater levels on Perth's Swan Coastal Plain, the species 'tolerant of excessive wetness' (see Havel 1968) displayed the greatest reduction in population size (Groom *et al.* 2000a). This included *A. fascicularis*, *P. ellipticum* and *H. angustifolium*. It was expected that as *A. fascicularis* and *P. ellipticum* are species restricted to winter-wet depressions (Marchant *et al.* 1987) such as damplands, they would be dependent on groundwater all year round, particularly during the dry summer period.

This study suggests that during a prolonged summer drought, neither *A. fascicularis* or *P. ellipticum* were accessing groundwater but were relying on soil moisture reserves. This also suggests that shallow soil moisture reserves (gravimetric content of 10–20%) were sufficient to sustain their summer water-use requirements, as both species were able to maintain summer stomatal conductances similar or greater than values obtained during the previous spring. The stable hydrogen isotope data show that *P. ellipticum* may have had access to groundwater in July 2001 (early winter) as a result of a small rise in winter groundwater levels, implying that the minimum accessible groundwater depth for *P. ellipticum* occurs between 1.39 to 1.45 m at this dampland.

Wetland water levels on Perth's coastal plain fluctuate seasonally, and some wetlands, including damplands, dry out by the end of summer. Damplands by definition are seasonally waterlogged basins (Semeniuk 1987); however, Perth's damplands do not always retain surface water, and was the case in 2000/2001 for the dampland studied in this paper. This may be due to below-average winter rainfall, reduced seasonal recharge and/or declining trends in regional groundwater level (Muir 1983; Townley *et al.* 1993). The trend for decreasing average rainfall currently being experienced by Perth may be part of a longer cycle (Davidson 1995). It has been predicted that by 2030 Perth may experience up to 10% less winter rainfall, and 5% more, or less, summer rainfall; by 2070, winter rainfall may decrease by 20% with summer rainfall increasing/decreasing by 10% (Anon 1996). Consecutive years of summer drought/poor winter rainfall can trigger extensive mortality of sandplain vegetation (Hnatiuk & Hopkins 1980; Groom *et al.* 2000b). If reduced winter rainfall translates into a lowering of summer groundwater levels and soil moisture content, then shallow-rooted species occurring in low-lying areas (*e.g. A. fascicularis, P. ellipticum*) will be particularly susceptible.

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Note from the Honorary Editor:

This column in the Journal of the Royal Society of Western Australia helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). References are abstracted from Current Contents by searching for Western Australia in the title and abstract. The references are separated into Physical Sciences and Biological Sciences.

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The effects of fire and quokkas (*Setonix brachyurus*) on the vegetation of Rottnest Island, Western Australia

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Abstract

Three different plant communities have dominated the vegetation of Rottnest Island over the past two centuries; low forest, *Acacia rostellifera* scrub, and sclerophyllous heath. In 1997 a fire burnt 90 ha of heathland and provided an opportunity to examine the relationships between dominant vegetation types, fire and grazing by quokkas (*Setonix brachyurus*). Our study and the literature indicated four major findings.

- Burnt heath recovered slowly if grazed. If not grazed, heath regenerated rapidly to become dense, tall and weed-free compared with the surrounding heathland, and the number of native species increased.
- Where there was no grazing, all three vegetation communities were able to become established immediately after the fire. Four and a half years after the fire, *Acacia* thickets dominated in some areas and reached 3-4 m in height, overshadowing a group of self-seeded *Melaleuca* seedlings and outcompeting heath species. It is anticipated that the *Melaleuca* will emerge and dominate when the shorter-lived *Acacia* declines, and that heath will continue to occupy open areas.
- The three dominant vegetation communities can be regarded as stable state alternatives. Heath will dominate if there is heavy grazing, as the young trees and *Acacia* are palatable and so cannot regenerate. Low forest dominates if there are only occasional widespread fires. Fire triggers the release of seed stored in tree canopies, and also temporarily reduces the local quokka population, giving seedlings a chance to become established. *Acacia* dominates if there are frequent fires and little grazing. Frequent fires stimulate *Acacia* to sucker from underground parts, while competition from tree species disappears, as trees are killed by fire, and if a second fire occurs before young trees set seed, they are eliminated locally.
- It appears that occasional widespread hot fires, presumably started by lightning, are likely to have occurred on Rottnest Island over the millennia before European settlement for *Melaleuca/Callitris* forest to have persisted.

Key words: Rottnest Island, vegetation, fire, quokkas, vegetation dynamics

Introduction

A row of islands lies off the coast of Perth, Western Australia, the largest of which are Rottnest Island (1900 ha) and Garden Island (1200 ha). These aeolianite limestone islands are remnants of Pleistocene dune ridges, left above sea level after the last post-glacial marine transgression. The vegetation of Rottnest and Garden Islands has strong similarities (Marchant & Abbott 1981). The majority of their native plant species are common to both islands, including the three tree species, *Melaleuca lanceolata*, *Callitris preissii* and *Pittosporum ligustrifolium*, as well as the tall shrub *Acacia rostellifera*. Small wallabies graze both islands, quokkas (*Setonix brachyurus*) on Rottnest Island and tammars (*Macropus eugenii*) on Garden Island. Over the past 200 years, the vegetation of Rottnest Island has been heavily exploited by humans to the point where the concept of 'natural' vegetation is almost irrelevant. However, fossil pollen data and historical reports over the last two centuries make it possible to trace changes in the vegetation types that have dominated the island, and the processes associated with the changes. The parallel with Garden Island, which has suffered less disturbance, serves as an additional check or reference point.

We attempt to find a conceptual framework for changes in the vegetation of Rottnest Island. The dynamics are studied from three aspects; the historical information is reviewed, the vital attributes of dominant species are assessed using criteria established by Noble & Slatyer (1980) with a view to predicting their response to a disturbance event, and the recovery of the vegetation after a fire in 1997 is examined.

Vegetation history

There have been significant changes in the vegetation of Rottnest Island since separation from the mainland

6500 years ago. Fossil pollen of native species dominant on the coastal plain today, such as fire tolerant *Eucalyptus*, *Casuarina*, *Banksia*, *Macrozamia* and *Xanthorrhoea*, have been found in the swamps on Rottnest Island, dating back to the early Holocene (Storr *et al.* 1959; Churchill 1960; Backhouse 1993). All of these genera became extinct on Rottnest after separation when a different set of influences came into operation.

There has been some uncertainty as to whether there were fires on Rottnest after the island was separated from the mainland and before European settlement. Abbott *et al.* (2000) suggested that the islands off Perth escaped anthropogenic disturbance, especially fire, for at least 5000 years, as the Aboriginal people did not use watercraft in this area (Abbott 1980). However occasional fires do appear to have occurred. Core samples taken from Barker Swamp reveal that layers of charcoal, which could only have resulted from fires, were deposited in the sediments. Backhouse (1993) discovered 14 charcoal bands laid down in the 1200 years between about 6850 and 5645 years before present indicating that fires occurred more than once per century. The frequency of the bands thereafter decreased to one per 350-400 years. The pollen record indicates that this decrease is because the fire-prone *Callitris* and *Eucalyptus* that had dominated the area disappeared from the catchment of the swamp and were replaced by a comparatively sparse low cover of *Pimelia* and Asteraceae. Other fires could have occurred elsewhere on Rottnest during this period. Groves (2001) separated large charcoal fragments (>1 mm) from small fragments (5-150 mm) in sediment cores from Barker Swamp, assuming that large fragments would indicate local fires on Rottnest Island while small fragments may have been transported on the wind from fires on the mainland. He concluded that major local fire events on Rottnest over the past 5300 years occurred about every 210 years while major regional fires (probably on the mainland) occurred about every 120 years. Unfortunately it is now difficult to resolve the question of the frequency of fires on Rottnest Island by studying cores from other catchments, because most of its swamps have been bulldozed to obtain marl for roadbuilding (Playford 1988; J Dodson, University of Western Australia, personal communication).

Today many of the native plant species on Rottnest and Garden Islands are killed by fire, including *Callitris* and *Melaleuca*, with regeneration only taking place through germination of seeds (Bell *et al.* 1987). In the absence of very frequent fires, the critical factors for vegetation are exposure to wind and salt, lower rainfall than the mainland with summer drought, and grazing by quokkas. Reports on the vegetation of Rottnest Island by visitors in the 17th and early 19th century mention the wooded nature of the island. In 1822 the botanist Cunningham reported that *Callitris* was abundant on the island 'to the point of monotony… occasionally relieved by … *Melaleuca* … and the more elegant *Pittosporum*' (quoted by Pen & Green 1983). Early reports of Garden Island described a similar picture. In 1827 Fraser reported areas 'thickly covered with cypress [*Callitris preissii*] and … extensive thickets of arborescent metrosiderous' [*Melaleuca lanceolata*], and in 1829 Fremantle noted that the vegetation was '… covered in a small kind of pine [*Callitris*] …. from the thickness of the trees and underwood it was impossible to move' (quoted by Wykes & McArthur 1995). However, Wilson described a very different landscape after a visit to the central southern part of Rottnest in 1829; '… miserably barren. The hummocks are sand hills, many of which are entirely destitute of any kind of herbage, in the valleys are some stunted trees and shrubs and very little grass' (quoted by Marchant & Abbott 1981). He had probably described the large blowout at Barnett's Gully, but his description also fits the desolation that follows fire on Rottnest Island.

In 1831 settlers started farming on Rottnest Island. In 1838 the prison was established and farming was intensified, with the introduction of pigs, horses, rabbits, sheep and cattle, and crops of wheat, barley, rye, stock fodder, fruit and vegetables, even tobacco and castor oil at times (Somerville 1976; Ferguson 1986). Wood was taken for fuel, and buildings and roads were constructed. Quokkas became scarce. The Aboriginal prisoners used fire to hunt them for food, and vice-regal parties hunted them for sport towards the end of the 19th century, as did tourists in the early 20th century (Storr 1963). The vegetation changed under the new regime of frequent fires, low wallaby numbers and removal of trees. In 1855, Jewell reported areas of dense scrub, *Acacia rostellifera* (quoted by Marchant 1977). In 1905, Lawson wrote that the interior of the island was covered with very dense *Acacia* scrub, quite impenetrable apart from the 'rides' that had been cut through it, and that trees were absent except in the settlement at the eastern end of the island and most of these were introduced (Lawson 1905). By 1919, Weir estimated that two thirds of the island (1200 hectares) was covered by *Acacia* scrub (Storr 1963), and in 1929 Glauert wrote that 'much of the island is clothed in dense wattle [*Acacia*] scrub' (quoted by Pen & Green 1983).

In 1917, legislation was passed prohibiting shooting on the island (Anon 1917), but shooting apparently persisted because in 1926 J B Stark was appointed Honorary Guardian under the Game Act 1912-13 (Storr 1963). New laws were promulgated in 1933 prohibiting firearms on the island altogether (Anon 1933). The quokka population recovered during this period, with an abundant food supply of nutritious *Acacia rostellifera* and palatable introduced plants associated with crops and improved pastures. By 1932 it was reported that quokkas were more numerous than before and were damaging crops (Storr 1963).

Overgrazing by quokkas prevented the regeneration of *Acacia* scrub, which by 1941 was fragmented and covered only 400 ha (Pen & Green 1983), one third of the area it had occupied 22 years earlier. In the mid-1950s, *Acacia* was even more restricted, to sheltered valleys and slopes (Storr *et al.* 1959). Here it was 3-6 m high, and often associated with the climber *Clematis linearifolia*. *Callitris* had apparently become so rare that it was not mentioned at all. The scrub was replaced by grassy heath consisting mainly of *Acanthocarpus preissii* and tussock grass *Austrostipa flavescens*.

In 1955 a major fire burnt two thirds of Rottnest Island, and a year later there was a widespread fire on Garden Island. The recovery of the vegetation on both islands was documented (Storr 1963; Baird 1958) and the effects of fire on the vegetation of the islands have been widely discussed since this time (White & Edmiston 1974; O'Connor *et al.* 1977; Hesp *et al.* 1983; Osborne *et al.* 1985; McArthur 1996a, b; 1998; Abbott *et al.* 2000).

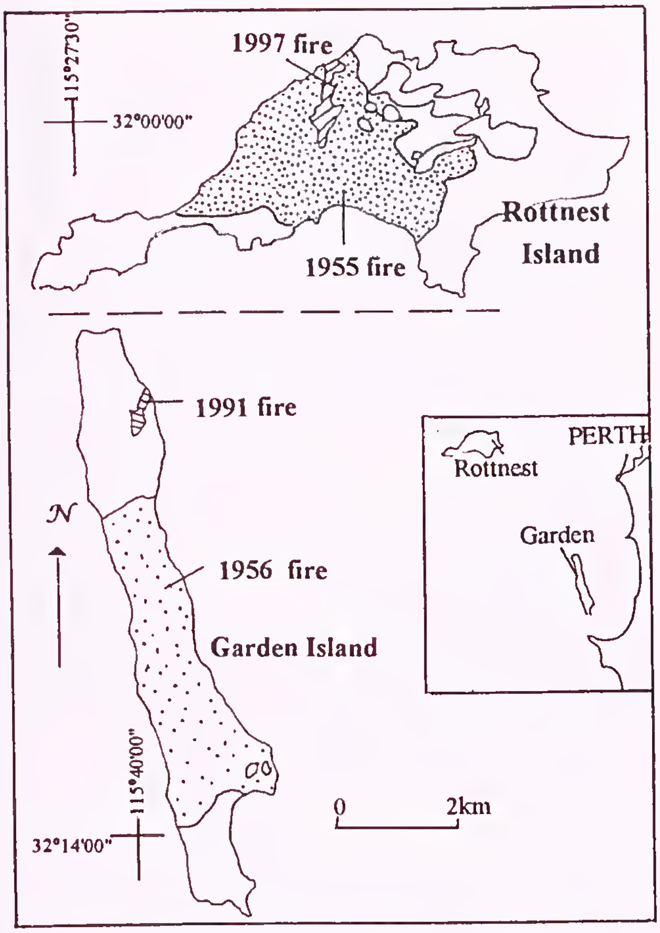

Figure 1. Location of major fires on Rottnest and Garden Islands since 1955.

During the latter half of the 20th century, the cover by forest and woodland was further reduced, to 7% by 1974 (White & Edmiston 1974), while heath became increasingly widespread. The primary management objective over this period was the provision of tourist amenities, as the island was an A Class reserve with the gazetted purpose of public recreation, with about 500 000 visitors per annum by the end of the century. Maintenance of the quokka population was another concern, as quokkas were endearing to tourists and also a declared threatened species. Fires were rapidly controlled if they occurred. A small fire on Garden Island in 1991 was studied in some detail (McArthur 1996a,b; McArthur 1998). A restricted fire on Rottnest Island in 1997 and the subsequent response of the vegetation is discussed in this paper. Fig 1 shows the positions of the four major fires on Rottnest and Garden Islands over the past fifty years; all fires occurred at the height of summer (end of January or during February).

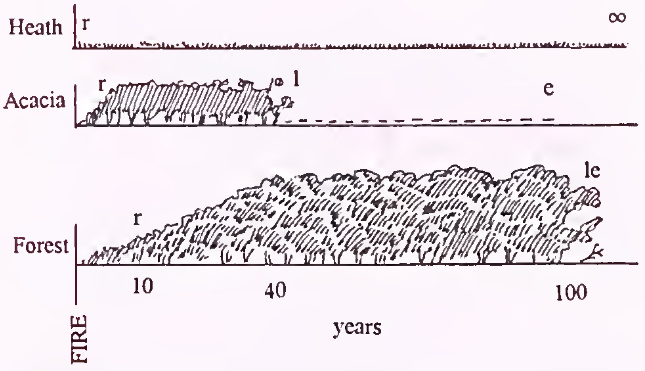

Figure 2. Vital attributes of the three dominant communities (r representing the time at which the species reaches reproductive maturity, l the end of the lifespan, and e the time at which all propagules, plants and seeds become extinct). After Noble & Slatyer 1980.

Attributes of dominant plant species on Rottnest Island

Melaleuca lanceolata/Callitris preissii low forest, *Acacia rostellifera* scrub and *Acanthocarpus* heath have dominated the Rottnest Island flora at various times. Noble & Slatyer (1980) suggested that successional changes in plant communities subject to recurrent disturbances can be predicted by examining the vital attributes of the dominant component species. Applying their criteria, *Melaleuca/Callitris* would be classified as CI (seeds are stored in the tree canopy not the soil, and germinants are intolerant of competition). Reproduction of *Melaleuca/Callitris* is solely propagule-based. These are bradysporous species with seeds stored in the capsules or cones in the canopy. The seeds are short-lived and there is no seedbank in the soil (McArthur 1996a). The trees are killed by fire, but dense germination in the vicinity of burnt parent trees can follow burning (Baird 1958; McArthur 1998; White & Edmiston 1974). They regenerate in open conditions, being unable to compete with conspecific adults. The trees take up to 10 years to reach sexual maturity (C Hansen, environmental officer, Rottnest Island Authority, personal communication), and their life span is about 110 years (McArthur 1998), although one *Callitris preissii* of about 140 years has been recorded (Powell & Emberson 1981). Fig 2 gives these vital attributes in diagrammatic form.

Acacia rostellifera falls into Noble & Slatyer's category of SVI (seeds are stored in the soil, but the species also reproduces vegetatively; germinants are comparatively intolerant of competition). The species germinates from seed and also resprouts after fire from underground parts up to 50 m distant from the parent plant (Storr 1963). *Acacia rostellifera* seeds are hard-coated and have a prolonged dormancy, in common with the great majority of *Acacias* (Simmons 1981). Successful regeneration requires open conditions such as follow disturbance, especially fire. The shrubs have a lifespan of about 40 years (Powell & Emberson 1981; McArthur 1996a), but become senescent on the islands after about 20 years (White & Edmiston 1974; McArthur 1996b).

The heath species *Acanthocarpus preissii* and *Austrostipa flavescens*, which together with the introduced *Trachyandra divaricata* make up two thirds of the vegetation cover in the heathland surrounding the burnt zone, are capable of regenerating vegetatively or from seed. *Trachyandra* is a rhizomatous herb, growing to 0.35 m, with ribbon-like leaves. These three dominant species are widespread on Rottnest Island and for the purposes of this analysis we assume that there is a constant supply of propagules from the surrounding heathland. *Acanthocarpus*, *Austrostipa* and *Trachyandra* are considered tolerant of competition as they continue to

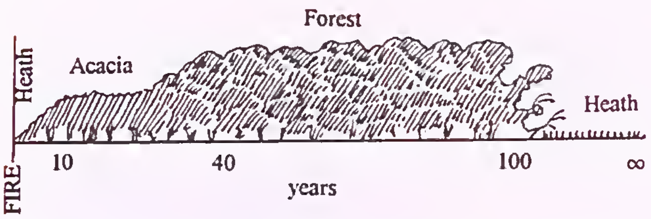

Figure 3. Vegetation replacement sequence for Rottnest Island forest-woodland-heath system following a fire, in the absence of further disturbance. After Noble & Slatyer (1980).

regenerate and are self-maintaining within an established heath environment, although they occur only occasionally as understorey species in dense *Melaleuca/Callitris* or *Acacia*. The fourth major component of the heath, *Thomasia cognata* (providing some 17% of vegetation cover) reproduces from seed alone. For this analysis, we classify the species of the heath as DT (seeds are dispersed widely so are available at any time, and seedlings are tolerant of competition).

A sequence can be predicted for the development of the three vegetation communities following a fire and in the absence of further disturbance except perhaps for light grazing (Fig 3). All species germinate or resprout immediately after fire. Most heath species regenerate from seed and rootstock, and reach maturity rapidly. The *Acacia* forms dense scrub 3-4 metres high within 5 years. Senescence starts at about 20 years (McArthur 1996b) with deterioration from the centre, and the plants die out by 40 years, leaving a seedbank in the soil for about 60 years or more. *Melaleuca* and *Callitris* are more slow-growing, but as the *Acacia* declines the forest species grow through and dominate until the last survivors die off at about 110 years. Thus, immediately following a fire and in the absence of further fire or grazing thereafter, all species would regenerate in the presence of seed and/or rootstock. The heath would dominate briefly before being overwhelmed by *Acacia* (Fig 3). The tree species would only grow through the *Acacia* as the latter thinned out and then died by 40 years of age. By about 110 years the *Melaleuca/Callitris* would have died leaving no seedbank, the *Acacia* seeds left in the soil would also have died by this time, and only the heath species would persist.

Materials and methods

Plant nomenclature is based on Pacskowska & Chapman (2000) and information from the Western Australian Herbarium.

Field survey

On 17th February 1997 a fire (started by a power pole) burnt through about 90 ha on Rottnest Island between the centre of the island and the north coast (Fig 4). The vegetation consisted of *Acanthocarpus* heath, apart from a small zone of coastal heath at the northern extremity (which is not considered in this survey). Several plantations adjoining the burnt area were protected from the fire by firebreaks, and the only trees burnt were two *Melaleuca lanceolata*. The burnt area and the immediately surrounding *Acanthocarpus* heath that was not burnt will be referred to as the Research Site. Within five months the Rottnest Island Authority had fenced 70% of the burnt area into six separate plots, using 1 m high fencing reputed to be quokka-proof for at least 8 years (C Hansen, Environmental Officer, Rottnest Island Authority, personal communication). Some quokkas were able to jump the fence but were removed periodically (C Wright, Environmental Manager, Rottnest Island Authority, personal communication). The entire fenced area was planted with *Melaleuca lanceolata* and *Callitris preissii* seedlings, of local provenance, over the ensuing four years at a density of about one plant per 20 m²; a few *Pittosporum ligustrifolium* were planted but none survived (C Hansen, Environmental Officer, Rottnest Island Authority, personal communication).

In August 2001, four sites were selected where the surrounding unburnt vegetation was in close proximity, and had a similar aspect to the area that had been burnt, within and outside the fenced plots. Further sampling was not possible because much of the burnt unfenced area surrounding the plots was taken up by fire breaks and vehicle access tracks. Three 25 m x 2 m transects were established at each site to compare the surrounding heathland that had not been burnt with the vegetation that had been burnt, both fenced and not fenced (Fig 4). Each of the 12 transects consisted of five 5 m x 2 m

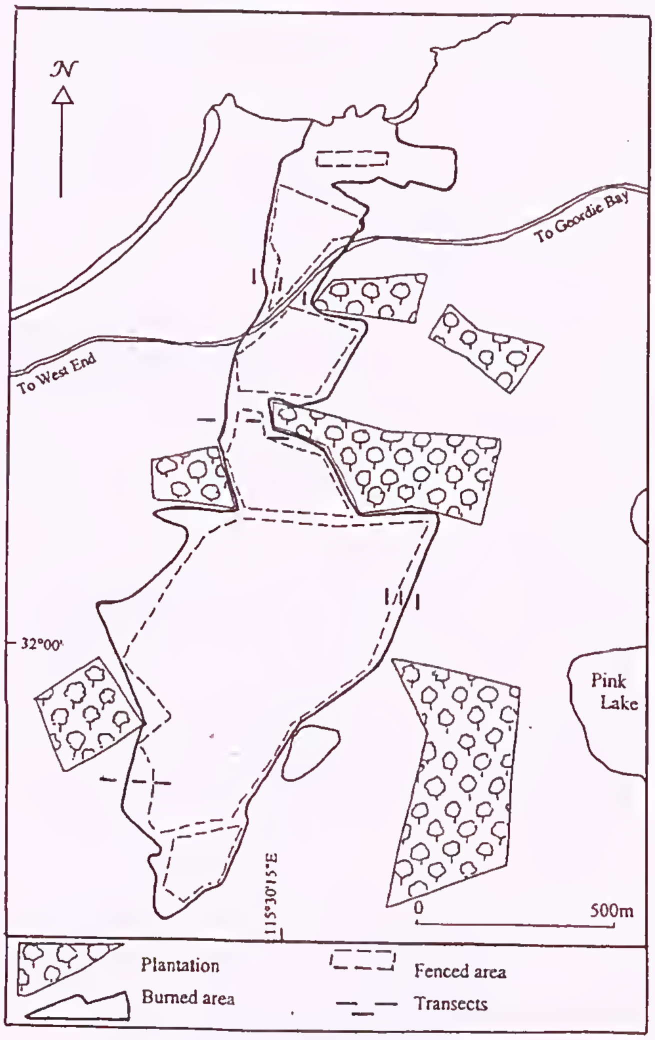

Figure 4. Rottnest Island: area burnt in 1997 showing fenced plots, adjacent plantations and positions of transects.

quadrats, for which the percentage cover and average height of each species present was recorded. The proportion of bare earth was also noted.

The three 'groups', burnt and fenced, burnt and unfenced, and unburned and unfenced were compared with regard to the number of native species, percentage cover of native species, and percentage cover of the introduced *Trachyandra divaricata*. Analysis of variance was used to test for significant differences amongst groups and transects. Logarithmic transformation was employed to stabilise the variance for species count data. The Kruskal-Wallis rank sum test was applied to the percentage cover data of both native species and *Trachyandra divaricata* because standard assumptions for ANOVA (in particular normality and homogeneity of variance) were violated.

Aerial photographs

Photocopies of the following aerial photographs were obtained from the Western Australian Department of Land Administration to assess vegetation changes on Rottnest Island, particularly at the Research Site.

- aerial photographs of Rottnest Island, 1942: black and white 29/9/42, Run 1 YX4140, YX4142; Run 3 YX 4155, YX4157, YX4159, YX4160, YX4162; Run 4 YX4136, and a copy of a map derived from these photographs: Australian Section Imperial General Staff 1943, Rottnest Island, 4th Australian Survey Co, RAE, scale approx: 1:16,000 (4 inches to 1 mile).
- aerial photographs of Rottnest a few days after the 1955 fire: black and white Run 1. WA 158. Scale 1:7920 taken 25/02/1955. These photographs were used to assess changes between 1942 and 1955. Subsequent vegetation changes were identified by comparing these images with aerial photographs taken in later years, by superimposing images which had been reduced to the same scale by photocopying. Photographs were: 8/4/1964 5114, WA 854, Rottnest Island (5112-5116) from 12,500', Project D60; 18/3/1967 5067 WA 1016, Rottnest Road Guide Revision Run 1 (5062-5069) 7920; 14/2/1972 5063 WA 1378 (C) Rottnest Island Run 1 (5059-5067) 7920 152.56; 1/2/1980 5018, WA 1857(C), Rottnest Island Run 1 (5014-5020) scale 1:10000, Job no 800001; 11/3/1990 WA 2851 (C), Rottnest Island Run 1 (50001-5010) Scale 1:15000, 900890.
- further series of aerial photographs was used to examine changes brought about by the 1997 fire; these comprised Rottnest Island, 6/2/1997 Metro regional area Run 41, 5002, 5004 and 5006, 1:20,000; an enlarged colour photocopy of aerial photograph 10/01/1998 WA 4044C; Perth regional area Metro photography project no 970000, Run 41:5003, Scale 1:25,000. Computer generated, enlarged images of aerial photographs were also obtained: Perth regional area Metro Photography 17/02/2000 Project no 990000, WA 4422C Run 41:5003, 1:25,000; 14/12/2000 Project no 000001, WA 4544C, Run 41:5139, Scale 1:25,000. Vegetation distribution was related to topography in the Research Site with the use of a photocopy of a contour map of Rottnest Island produced by the Department of Lands and Surveys, Job no 800001, 1m contours, from photography taken February 1980 and October 1981.

Results

Field survey

The vegetation of the surrounding *Acanthocarpus* heath that had not been burnt consisted almost entirely of three native species, *Acanthocarpus preissi*, *Austrostipa flavescens*, and *Thomasia cognata*, and the introduced *Trachyandra divaricata* (Table 1). Burning of *Acanthocarpus* heath

Table 1

% cover and frequency of plant species in burnt and fenced, burnt and unfenced, and unburnt areas.

	Burnt and fenced		Burnt and unfenced		Unburnt	
	% cover	% Freq	% cover	% Freq	% cover	% Freq
Acanthocarpus preissii	7	70	21	100	32	100
Austrostipa flavescens	26	100	19	100	14	95
Thomasia cognata	15	80	8	60	15	75
Olearia axillaris	8	60	0		0	
Acacia rostellifera	29	60	0		0	
Solanum symonii	1	25	1	25	0	
Lepidosperma gladiatum	4	15	1	20	0	
Lepidosperma pubisquameum	3	20	0		0	
Carex preissii	0.2	5	0.2	30	0	
Conostylis candicans	3	40	5	55	3	50
Rhagodia baccata	4	15	0		0	
Guichenotia ledifolia	0.05	5	2	20	3	15
Trachyandra divaricata	1	45	11	95	14	80
Planted *Melaleuca* and *Callitris*	7	35	N/A		N/A	
Seedlings of ephemerals	3	100	9	100	8	100
Bare	8		23		11	
TOTAL	>100[a]		100		100	

[a] *Acacia rostellifera* formed a canopy with an understorey, so that the total coverage shown for burnt and fenced sites is greater than 100%. The understorey consisted almost entirely of native species, so the understorey was disregarded when calculating percentage cover of native species for the statistical analysis.

Table 2

Number of native species and percentage cover of various types, with 95% confidence intervals (n = 20 quadrats, over 4 transects).

	Burnt fenced	Burnt unfenced	Unburned unfenced
Number of native species	5.6 (4.9-6.3)	4.3 (4-4.6)	3.6 (3.3-3.9)
% cover of native species	91 (89-93) %	57 (51-63) %	68 (61-75) %
% cover of *Trachyandra*	1 (0-2) %	11 (7-15) %	13.7 (11.7-15.7 %)
% cover of introduced species (including *Trachyandra*)	4.5 (3-6) %	20 (15-25) %	22 (15-29) %
% Bare earth	4.5 (2.5-7) %	23 (19-27) %	10.5 (7.5-13.5) %

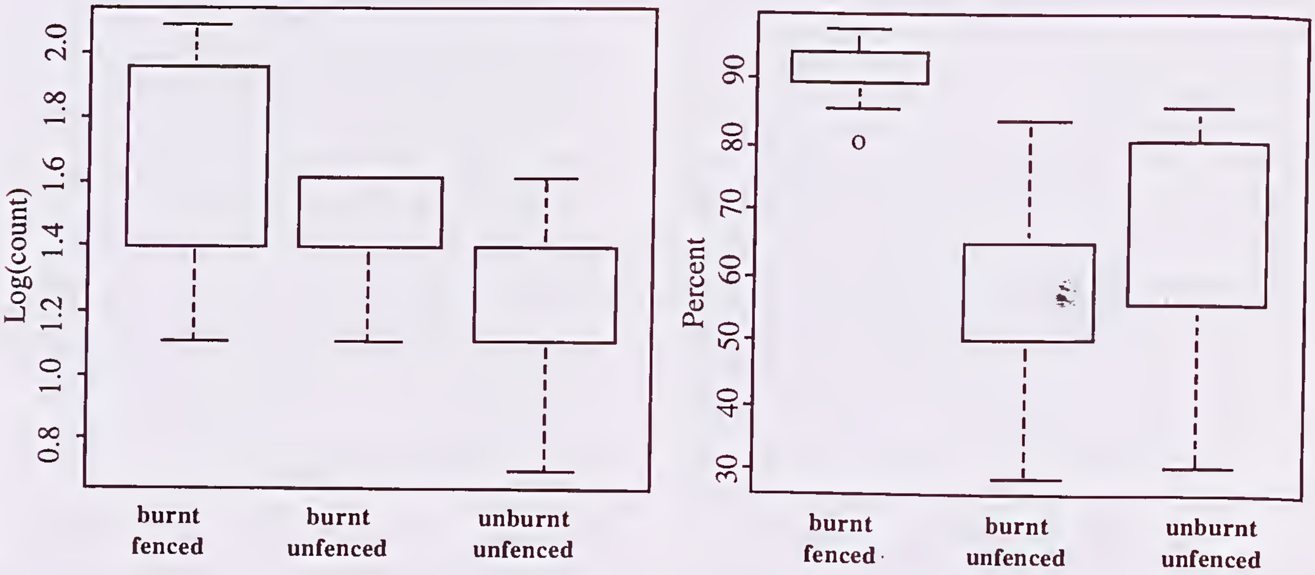

Figure 5. A: Number of native species in the three areas (burnt fenced, burnt unfenced and unburnt unfenced). B: % cover by native species in the three areas (burnt fenced, burnt unfenced and unburnt unfenced).

increased the number of native species present, particularly if the area was fenced against quokkas (Table 2; Fig 5A). The ANOVA for log of species count was highly significant for different groups ($P < 0.001$). The percentage cover of native species in the three areas also showed significant differences ($P < 0.001$; Table 2). In unfenced and unburned heath, percentage cover of native plants was variable (Fig 5B). Where the heath had been burnt but not fenced, cover was low indicating that where quokkas could graze the new growth the vegetation had not recovered even after 4.5 years. By contrast the cover of native species in burnt areas fenced against grazing was high.

Melaleuca/Callitris

Melaleuca lanceolata and *Callitris preissii* trees growing in plantations adjacent to the burnt area were not burnt but two isolated *Melaleuca* trees and one *Pittosporum ligustrifolium* were burnt. One of the *Melaleucas* was included in the quokka-proof fencing subsequently erected, and numerous *Melaleuca* seedlings germinated to the west side of this tree after the fire (although not within the sampled quadrats). These self-seeded *Melaleucas* grew much more rapidly than the planted *Melaleuca* seedlings. The second burnt *Melaleuca* tree was not fenced and no seedlings were observed growing in its vicinity. The *Pittosporum* tree that was burnt was just outside one of the fenced plots. This species is capable of sprouting from damaged roots after fire (McArthur 1996a) but in this case did not do so. No seedlings were observed outside the fence, but 76 young *Pittosporum* 30-40 cm high were growing within the fence to the west of the burnt tree in August 2001 (C Hansen, Environmental Officer, Rottnest Island, personal communication). *Melaleuca lanceolata* and *Callitris preissi* planted in the four years following the fire were noted in all transects within fenced areas, and formed some 7% of cover in those transects (Table 1).

Acacia rostellifera

The most striking contrast between the vegetation of the three areas was the dense germination and growth of the native *Acacia rostellifera* within enclosures, reaching 5 m height on sheltered slopes. It had not grown in the research site for over 40 years prior to the 1997 fire. However, patches of acacia scrub had grown there between 1942 and 1955, decreasing in extent until eliminated after the 1955 fire (Figs 6A,B). The distribution of *Acacia rostellifera* in 2000 (Fig 6C) corresponded with that 60 years earlier, in 1942. Comparison of the distribution of acacia after the 1997 fire with a contour map showed that the species had germinated in swales and on east-facing slopes (Fig 7).

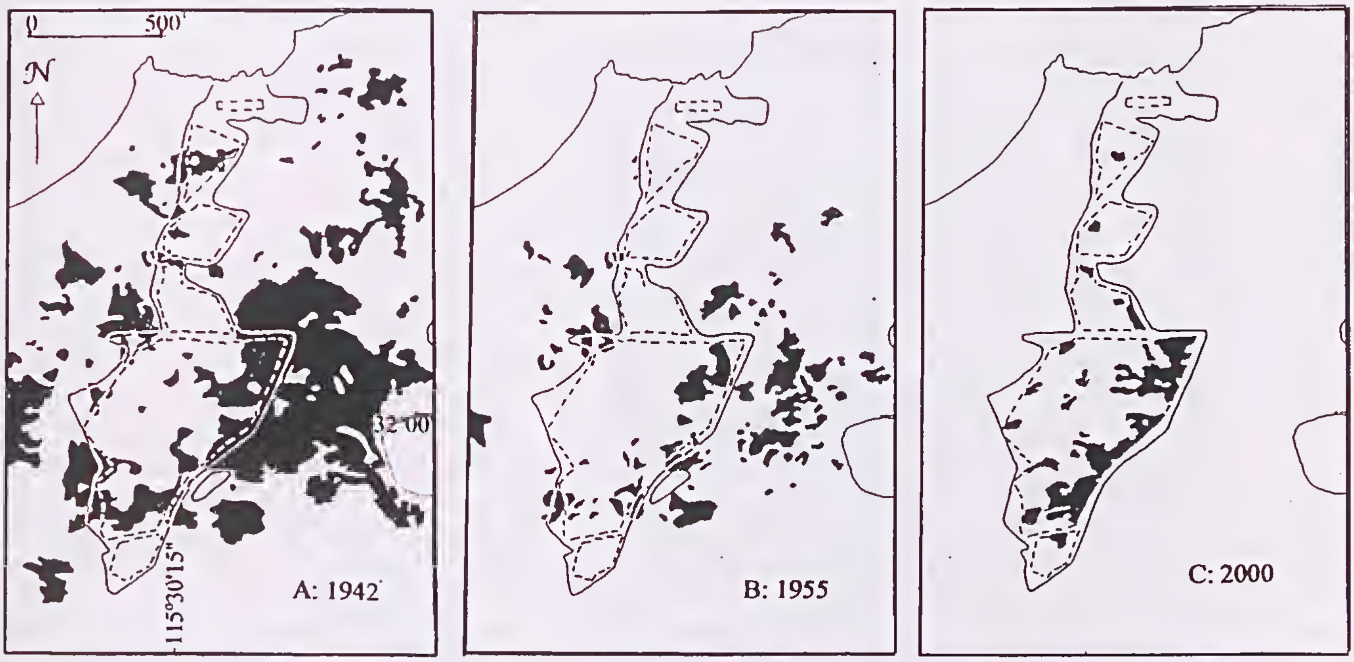

Figure 6. A: Distribution of *Acacia rostellifera* in 1942. B: Distribution of *Acacia rostellifera* in 1955. C: Young growth of *Acacia rostellifera* in the enclosures. The only acacia in the area between 1956 and 1997 was in plantations.

Heath species

Additional native species recorded in burnt areas but not in the unburnt heath were *Rhagodia baccata*, *Olearia axillaris* and *Lepidosperma pubisquameum* only within enclosures, and *Solanum symonii* (a fire ephemeral, mostly dead by the time of the survey), *Lepidosperma gladiatum* and *Carex preissii* within and outside enclosures (Table 1).

The increased coverage by native species in enclosures was at the expense of *Acanthocarpus preissii*, the introduced *Trachyandra divaricata* and (to a lesser extent) small introduced annuals, notably *Euphorbia peplus* and the grass *Lagurus ovatus*. *Trachyandra* was an important component of the vegetation in unburned and unfenced heath (Table 2; Fig 8) but little *Trachyandra* persisted within enclosures (Kruskal-Wallis test, P<0.001).

Discussion

The vegetation recovery sequence proposed by Noble & Slatyer (1980) seems applicable to the dominant communities on Rottnest Island. The 1997 fire was followed by germination or regeneration of all dominant communities within fenced areas.

Melaleuca/Callitris.

The only germination observed of these species was beside a burnt *Melaleuca* within an enclosure, despite the fact that *Melaleuca* and *Callitris* trees were growing in plantations, which had not been burned, within 50 m of the fenced plots. Four and a half years after the fire the slender saplings reached 2 m high but were far outstripped by young *Acacia rostellifera*. It was anticipated that *Acacia* would overshadow these trees for another twenty or thirty years. At Woodman Point thirty years after a fire, a stand of senescent 5 m *Acacia rostellifera* was still taller than *Callitris preissii* trees but the *Callitris* were young at 30 years of age, and would shortly displace the *Acacia* (Powell & Emberson 1981). On Garden Island, progress of the forest trees could be traced over their life span as the ages of various stands of *Callitris/Melaleuca* trees were known from the dates of fires that stimulated their germination. It was found that forty year old trees numbered approximately 16 per 25 sq m, 75 year old trees numbered 6, and hundred year old trees only 1 per 25 sq m. As the decline progressed the forest was replaced by *Acanthocarpus preissii* heath (McArthur 1998).

Acacia rostellifera

This dominated parts of the Research Site enclosures, reaching 3-4 m. The changing distribution patterns of this species since 1942 have been mentioned. The decrease in *Acacia rostellifera* between 1942 and 1955 (Figs 6A,B) accords with Storr's report of major and continuing fragmentation of *Acacia rostellifera* scrub from the 1930s onwards (Storr 1963). The disappearance of *Acacia* from around Barker Swamp after the fire of 1955 was explained by Storr (1963) who recorded that there had been an abnormally high number of quokkas in this area after the fire. Small pockets of scrub had escaped the fire here, and within two years the quokkas surviving in these nodes had eaten all regenerating *Acacia*, and the scrub had been completely replaced with *Acanthocarpus* heath. The only *Acacia* in the area at the time of 1997 fire was in surrounding plantations, established between 1964 and 1972. The resemblance between the distribution patterns of *Acacia rostellifera* in 1942 and 2001 suggests that after the fire *Acacia* had grown from seed in the soil,

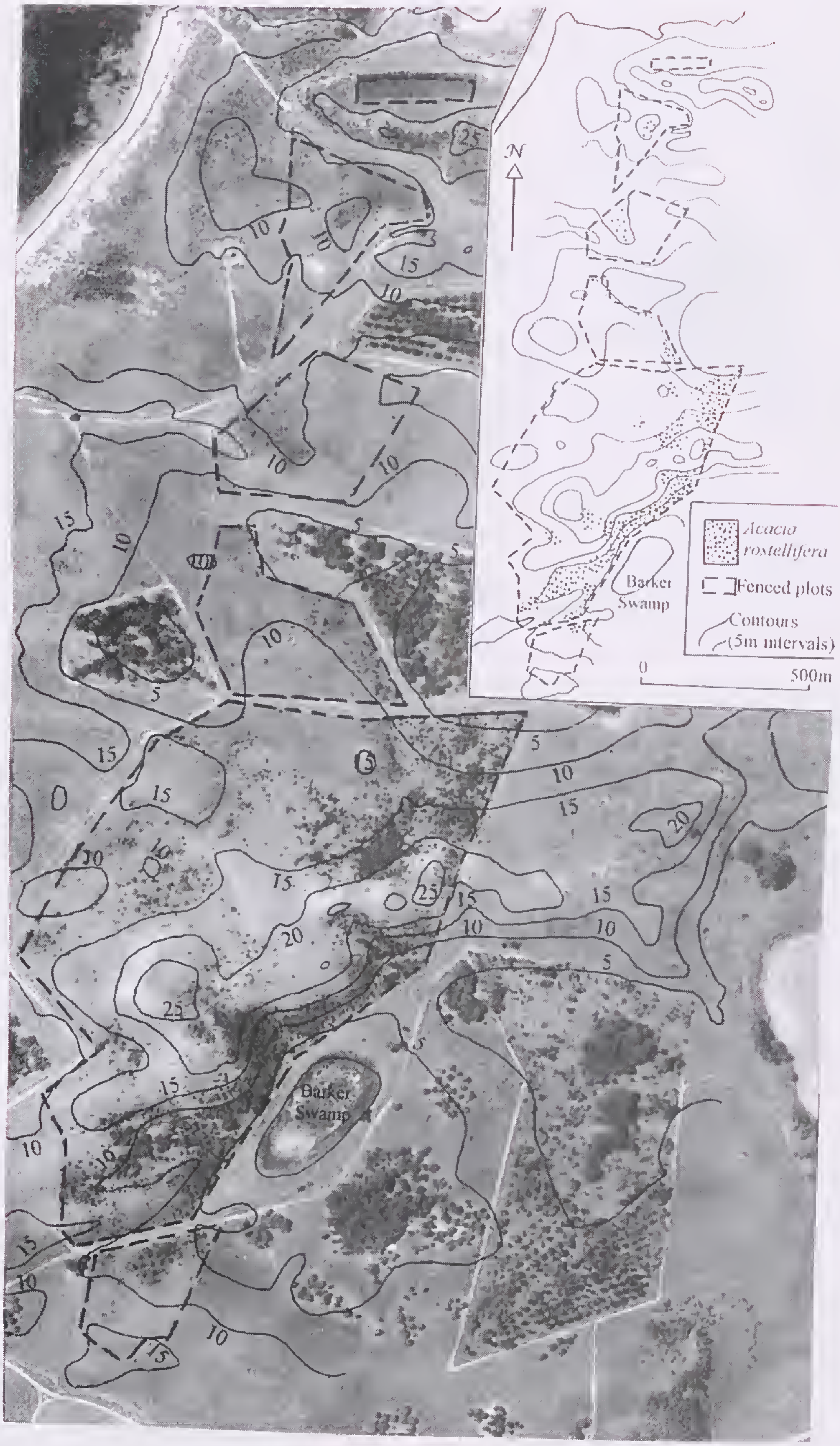

Figure 7. Growth of *Acacia rostellifera* in February 2000 in relation to topography.

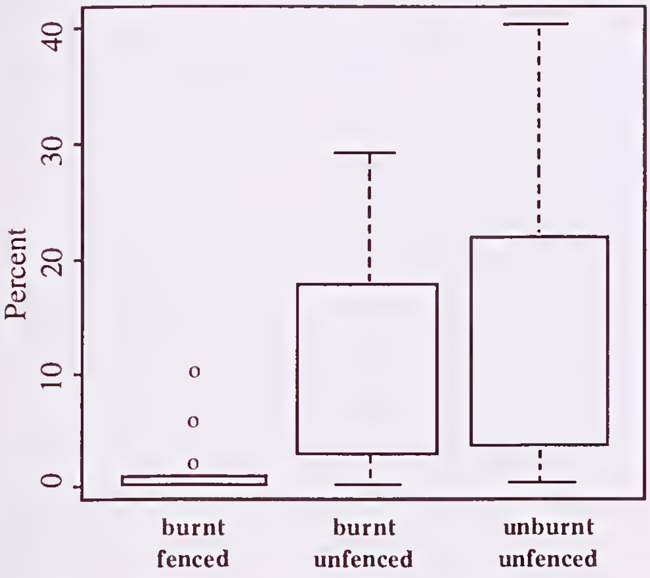

Figure 8. % cover by the introduced *Trachyandra divaricata* in the three areas (burnt fenced, burnt unfenced and unburned unfenced).

deposited some 60 years previously. Germination triggered by the 1997 fire in areas outside enclosures presumably succumbed to grazing.

The relationship between the distribution of *Acacia* within the enclosures and topography, with growth restricted to swales and east-facing slopes could be associated with the fact that the senescent parent *Acacias* of the 1940s and 1950s are likely to have survived longest in favourable sites.

Acanthocarpus heath

This was the most widespread vegetation community throughout the burnt area at the time of the survey, dominating except in areas of *Acacia rostellifera*.

Fire and marsupial grazing/browsing

The basic model of Noble & Slatyer (1980) illustrates the development of the vegetation communities of Rottnest Island after a single disturbance event. However if the vegetation dynamics are considered in terms of two major factors, fire and marsupial grazing, then a second model of alternative stable states becomes useful.

Charcoal deposits indicate that infrequent fires have occurred on Rottnest Island over the 6500 years since separation from the mainland (Backhouse 1993; Groves 2001). Presumably these would have been initiated by lightning, concurring with summer and drought years. Fires occurred about every 200 years in the vicinity of Barker Swamp alone (Groves 2001). Hopkins *et al.* (1985) suggested that infrequent major conflagrations take place on islands where there is no Aboriginal presence. Fires are known to be started by lightning on islands in the Recherche Archipelago (Weston 1985; A Hopkins, Department of Conservation & Land Management, Woodvale Research Centre, personal communication; M Fitzgerald, Department of Conservation & Land Management, Esperance, personal communication). Fires caused by lightning strikes are not uncommon on the Perth coastal plain, and it is likely that these could have occurred more than once per century on the islands (R Smith, Wildfire Prevention, Fire and Emergency Services Authority of Western Australia, personal communication).

These fires could have been fierce and widespread in woodland areas, as a considerable amount of flammable material presumably had accumulated. Total available fuel in mature *Melaleuca* forest has been estimated at 15-25 tonnes ha^{-1}, and in *Acacia rostellifera* scrub 30 t ha^{-1} (McArthur 1996a). This is a heavy fuel load in view of the fact that the maximum loading that can be handled by a bush fire fighting brigade on a normal summer day is 8 t ha^{-1} (M Cronstedt, Fire and Emergency Services Authority, personal communication).

There is also doubt as to whether communities of *Callitris/Melaleuca* or *Acacia rostellifera* could have persisted indefinitely in the absence of fire. McArthur (1996b) suggested that *Callitris* and *Melaleuca* very rarely regenerate other than in the vicinity of burnt parent trees. In the Research Site, germination of *Melaleuca* was restricted to the vicinity of a burnt *Melaleuca* within a fenced plot. Seed-bearing cones of *Callitris preissii* were scattered in one fenced plot but failed to produce any seedlings (C Hansen, Environmental Officer, Rottnest Island Authority, personal communication). However, *Callitris* and *Melaleuca* can sometimes reproduce without fire; in 2000 they germinated on Rottnest Island at Oliver Hill, where seed-bearing branches of the two species had been laid down to stabilize a small blow-out. Some *Callitris preissii* also germinated in the absence of fire on the mainland coast at Woodman Point (Powell & Emberson 1981).

McArthur (1998) reported that *Acacia* may regenerate without fire, mainly from root suckers, and can even be rejuvenated if seasonal conditions and the insect load permit. *Acacia rostellifera* can regenerate from rootstock after damage to the above ground parts along footpaths or after destruction by nesting cormorants, but there is not the massive germination and regeneration that follows fire. Fire appears to trigger germination and possibly reduces insect numbers.

Melaleuca, Callitris and *Acacia* are palatable to quokkas, and in the presence of a large quokka population regeneration rarely occurs (Storr 1962). Planted specimens do not survive unless fenced. Palatable species can become established however after a widespread fire as macropod grazing can be reduced for a time (Whelan & Main 1979). Baird (1958) found virtually no signs of grazing for two years along the southern margin of the huge 1956 fire on Garden Island. After the 1955 fire on Rottnest Island, some sites were almost completely deserted by quokkas (Storr 1963). This may be because resident quokkas are killed by fire (McArthur 1996a) or because there is no shelter for too great a distance (Storr 1963). The influence of grazing by macropods on the survival of seedlings is not fully understood. The occurrence of highly palatable plant species in an area or strong territorial instincts on the part of the animals can affect the ranges of grazing animals after fire (Whelan & Main 1979).

Acanthocarpus heath is self-maintaining under a regime of heavy grazing, although at a suppressed level. In those areas burnt in the 1997 fire but not enclosed against grazing, almost a quarter of the area was still denuded after 4½ years. The heath within enclosures after the 1997 fire appeared rejuvenated, and resembled the more diverse heath described in the 1950s (Storr 1959), while that surrounding the burnt area resembled the more degraded heath described in the 1980s (Hesp *et al.* 1983). In the 1950s there were *Acanthocarpus preissii* with *Austrostipa flavescens*, and two less common tussock grasses *Poa caespitosa* (probably *Poa poiformis*) and *Danthonia caespitosa* (probably a misidentification of *Austrodanthonia occidentalis* - M Hislop, WA Herbarium, personal communication), *Acacia rostellifera*, the sedges *Lepidosperma gladiatum*, *L. pubisquameum* and *Carex preissii* and *Conostylis candicans*. Dicotyledons were uncommon, with *Thomasia cognata*, *Guichenotia ledifolia* and *Trachymene coerulea* in disturbed areas. By the 1980s heath was described as the most widespread community on the island, covering about one-third of the island's area and the species list was reduced to *Austrostipa*, *Acanthocarpus*, *Thomasia*, *Guichenotia* and *Conostylis* but with the notable addition of the introduced *Trachyandra divaricata* (Hesp *et al.* 1983). In 2001 these were the species found in the heath surrounding the burnt site.

The native heath appears to be resilient, as *Trachyandra divaricata* was the only introduced perennial species noted in the Research Site after 180 years of settlement and the introduction of many other alien species. It is a primary coloniser of disturbed and unvegetated areas, and is known to be toxic to horses and unpalatable to quokkas (J Dodd, Department of Agriculture, WA, personal communication). *Trachyandra* was present on Rottnest in the 1960s but seldom occurred away from coastal dunes (Storr 1962); White & Edmiston (1974) expressed concern that the heath was being replaced by *Trachyandra*, and by 2001 it was an important component of the surrounding unburned heath in the Research Site. The species appears to persist with continued disturbance but to give way to competition from native species if disturbance ceases.

Alternative stable states

Vegetation dynamics may be usefully represented in terms of alternative stable states (Sutherland 1974; May 1977; Laycock 1991; Law & Morton, 1993; Hobbs 1994; Noble 1997). Transitions between states occur if there are specific changes in prevailing conditions. *Melaleuca/Callitris* forest, or *Acacia rostellifera* scrub or *Acanthocarpus* heath, can dominate on Rottnest Island depending on the circumstances (Fig 9).

If there were occasional hot fires, then low *Melaleuca/Callitris* forest would dominate. The dense shade of this forest has little understorey, so the quokka population would remain comparatively small. Fires would tend to be intense and infrequent but widespread, fuelled by accumulated litter so that parts of the island would be free of quokkas for a time after burning, and palatable tree species would escape grazing until they were large enough to withstand it.

Under conditions of frequent fires and little grazing, *Acacia* scrub would dominate; no shrub on Rottnest recovers as well after fire as *Acacia rostellifera* (Storr 1963). Frequent fires eliminate *Melaleuca/Callitris* locally, as two fires within about 10 years could kill mature trees and then their offspring before they reached reproductive age, leaving no propagules to germinate.

With heavy grazing, *Acanthocarpus* heath would

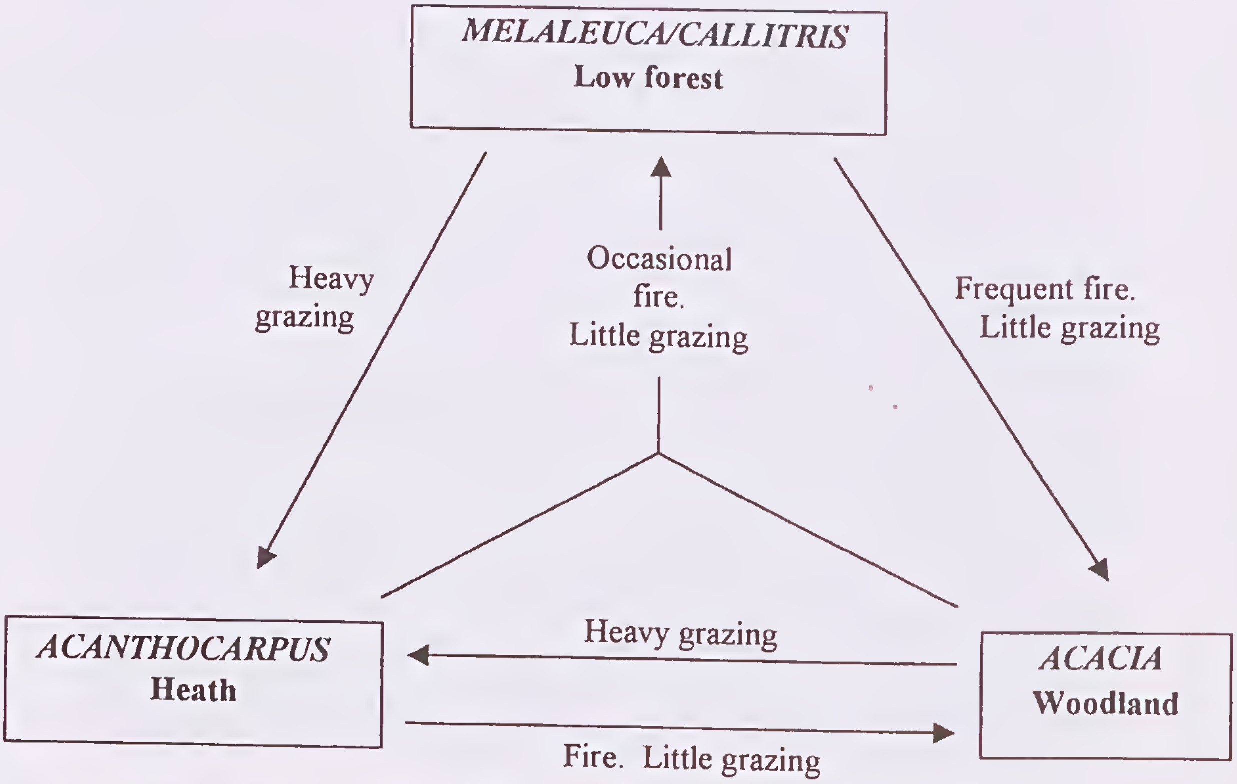

Figure 9. Alternative stable states model for Rottnest Island.

dominate. *Acacia rostellifera* is a favoured food for quokkas, and *Callitris* and *Melaleuca* are very palatable, and a large quokka population would destroy shoots and seedlings as they appeared so that these species would die out with the death of the mature plants.

The transitions from one stable state to another have been precipitate over the past 200 years, brought about by human intervention. It is postulated that there were occasional large fires before human occupation in 1838, and that these were associated with *Melaleuca/Callitris* forests. These gave way to *Acacia rostellifera* scrub between 1840 and the 1920s/1930s, when frequent fires took place and the quokka population was kept low by hunting. After this the quokka population was protected and burgeoned; the population probably reached saturation point by the mid twentieth century. Heathland predominated with this heavy grazing, and the prevention or control of fires after 1955.

It is possible that the *Acanthocarpus/Austrostipa* heath is not stable, but is becoming increasingly degraded by invasion by *Trachyandra divaricata* and by overgrazing and damage by quokkas. The stable state concept does not preclude the possibility that future changes might occur to the vegetation, associated with changes in the island environment or invasion by other species.

It would seem that virtually all of the natural old growth trees on Rottnest must be drawing towards the end of their life span. Quokkas were protected from 1917 and there had been some limitations on quokka hunting prior to this (CSO File 2047/1900 in Joske *et al.* 1995), with the result that presumably little regeneration of trees could have taken place for 80 years. *Melaleuca/Callitris* forest thins out rapidly from 80 years of age and the trees disappear within about thirty years. Similarly, if quokka grazing prevents regeneration of *Acacia rostellifera*, then *Acacia* scrub senesces and dies in 20-40 years.

The exploitation of the vegetation of Rottnest Island for two centuries releases environmental managers to some extent of expectations that they should restore the vegetation to any 'original' state. This gives considerable freedom of action, but in practice severe constraints are imposed by the island's gazetted purpose of 'public recreation', and by the threatened status of quokkas, which are a Western Australian icon. Both of these factors restrict the use of fire as a management tool, and it is interesting to note that the Draft Management Plan for the island for 2002-2007 states that 'fire is a threat to all habitats ... particularly ... to woodland communities'. However from our study, it is clear that fire remains an important factor shaping the vegetation and that its occurrence (or that of a suitable alternative disturbance), in conjunction with local control of quokka grazing may be essential for the maintenance of some of the major vegetation types (outside plantations) on the island.

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Stratigraphy and origin of regolith in the East Yornaning catchment, south-western Yilgarn Craton, Western Australia

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Abstract

Using a lithostratigraphic approach, the regolith within the East Yornaning catchment is subdivided into two major units of weathered Precambrian bedrock origin and a further four major units of sedimentary origin. The oldest sedimentary unit is the Westonia Formation, a mainly crudely stratified, light red clayey quartz sand, deposited along valley side-slopes by unconfined sheet-wash during the middle–late Tertiary. Unconformably overlying the Westonia Formation and weathered bedrock with a gradational contact is the Mulline Formation, a mainly dark red, pisolitic, quartz sandy aluminous duricrust. Petrographic and granulometric analyses indicate that the Mulline Formation is a secondary or "overprint" lithofacies, developed within upper sections of the Westonia Formation and weathered bedrock largely as a result of the allogenic addition of fine-grained quartz. Weathered basement and the Mulline and Westonia formations are unconformably overlain by the Gibson Formation, a dominantly light grey, massive, bimodal quartz sand, deposited as aeolian sand sheets during arid phases coeval with high latitude glaciations in the Pleistocene. Completing the sedimentary sequence and underlying most of the landsurface is the Nuendah Formation, a mainly grey, crudely stratified, muddy quartzo-feldspathic sand. The Nuendah Formation ranges in age from the present where it is forming along valley floors and side-slopes by fluvial and colluvial processes, through to the early Quaternary where it fills small palaeovalleys situated beneath the present major valley floors. The sequence of Gibson Formation grey sand overlying Mulline Formation pisolitic duricrust overlying Westonia Formation red clayey sands resembles the uppermost zones of a granitic deep weathering profile. Careful examination of regolith strata on a case by case basis is required for reliable interpretations of regolith genesis.

Introduction

A complex regolith covers much of the Precambrian bedrock along the south-western margin of the Yilgarn Craton in Western Australia (Simpson 1912; Prider 1966; Finkl & Churchward 1973; Anand & Paine 2002). Many aspects of the regolith in this region have been studied in considerable detail, including the development of weathering profiles over different bedrock types (Sadlier & Gilkes 1976; Davy 1979), the alteration of primary minerals at the weathering front (Gilkes & Suddhiprakaran 1979; Anand *et al.* 1985), the mineralogical properties of aluminous and ferruginous duricrusts (Grubb 1966; Anand *et al.* 1991), the near-surface geochemical expression of bedrock mineralization (Davy & El-Ansary 1986), the hydrological characteristics of weathered bedrock aquifers (George 1990), the relationship between regolith, soils and landforms (Mulcahy 1960; McArthur *et al.* 1977), and the nature and origin of surficial Mesozoic and Cenozoic sedimentary strata (Finkl & Fairbridge 1979; Salama 1997). No studies, however, have documented in any great detail the major lithological properties, stratigraphic relationships and origins of all regolith strata within an entire hydrological catchment.

A major advantage of including all strata in a geological study of the regolith is that it provides a basis for the distinction of units produced by the *in situ* chemical weathering of crystalline basement rock from those units produced by sedimentary processes. Owing to close similarities in texture and composition between weathered basement and overlying sediment, and the poor preservation of primary sedimentary and igneous structures, unconformable contacts between the two major regolith types may easily escape detection. Furthermore, as will be demonstrated here, traditional models used to infer regolith type and origin from landform and landscape position are often unsatisfactory, and it is only through a detailed study of regolith strata on a case by case basis that reliable interpretations of regolith genesis can be made.

Using a non-genetic, lithostratigraphic approach (Salvador 1994), the regolith within the East Yornaning catchment is subdivided into six major units, two of which are interpreted to have formed by the *in situ* weathering of Precambrian bedrock (granite and dolerite), and four of which are interpreted to be of sedimentary origin. The latter are correlated with formations formally established by Glassford (1987) for sedimentary regolith in the north-eastern and central Yilgarn Craton. Correlations with other relevant lithostratigraphic schemes are, however, also considered for the sake of completeness. The origins and ages of the regolith units are also discussed. However, formational ages, whether they relate to deposition, weathering or some other form of near-surface alteration, are typically poorly constrained.

Nomenclature

Following Eggleton (2001), the term "regolith" is used here to refer to the entire succession of earth materials overlying fresh bedrock, which in the context of the south-western Yilgarn Craton generally equates to Precambrian granite, gneiss or dolerite (see below). The regolith therefore includes materials of widely different colour, induration, structure, fabric, texture, composition, age and origin.

Some regolith "lithofacies", *i.e.* materials of similar lithological composition, stratigraphic position and presumably also genesis, may be produced by the chemical weathering of Precambrian basement. Other lithofacies may be distinct primary sediment types (that need not be weathered), whereas others still may be produced by alteration processes that overprint weathered bedrock and sediment in a like manner and therefore pass from one regolith type to the other with only a subtle change in lithological properties. A good example of this is ferruginous or aluminous "duricrust", which is an indurated, generally nodular to pisolitic lithofacies rich in secondary iron or aluminium minerals

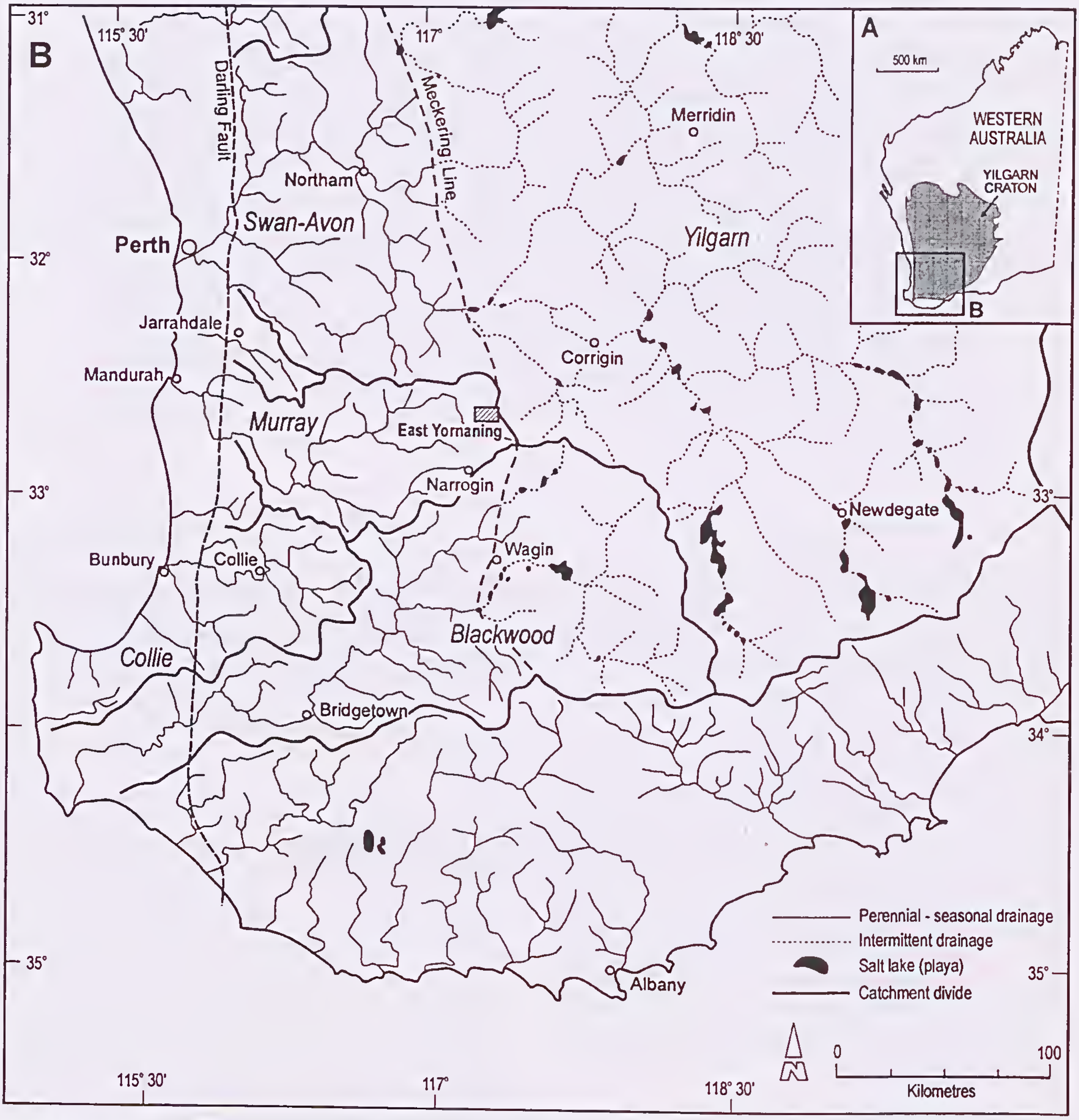

Figure 1. Regional setting of the East Yornaning catchment. A: Location of the south-western Yilgarn Craton within Western Australia. B: Location of the East Yornaning catchment within the south-western Yilgarn Craton. Major drainage basins and eastern limit of incised drainage (Meckering Line) also shown. Modified after Mulcahy (1967) and Beard (1999).

that acts as a protective cap for other less indurated regolith materials at the landsurface. Woolnough (1927), who coined the term duricrust, believed it to be the product of deep weathering under conditions of strongly seasonal rainfall and perfect peneplanation, but it is used here purely as a descriptive term without genetic connotation. Another term, frequently used synonymously with the ferruginous form of duricrust, is "laterite", but I avoid the use of this term owing to numerous conflicting opinions as to its meaning (Terrill 1956; Bourman 1993; Eggleton & Taylor 1999). A similar problem exists with the term "ferricrete", which in South Australia is generally used to describe iron-rich surficial materials regardless of their origin (Milnes *et al.* 1985; Bourman 1993), but in Western Australia is commonly used for detrital sediments that have been impregnated and cemented by iron oxides and oxyhydroxides (Anand 1998; Anand & Paine 2002).

General setting

The East Yornaning catchment comprises an area of about 14 000 ha within the western margin of the wheatbelt, bounded by latitudes 32°39' and 32°46' S and longitudes 117°11' and 117°25' E (Fig 1). The catchment is elongate in an E–W direction and is drained by a fourth-order tributary (*sensu* Strahler 1952) of the Hotham River, in the upper reaches of the Murray drainage basin (Fig 1). Its eastern interfluve is shared with the Swan–Avon drainage basin (Beard 1999) and, more importantly, also forms part of the Meckering Line (Mulcahy 1967). Originally delineated by Jutson (1934), this NNW–SSE trending zone marks the transition from relatively steep-sided, narrow-floored and high-gradient valleys in the west, to much broader and flat-floored valleys locally occupied by chains of salt lakes (playas) to the east (Fig 1).

Most workers (*e.g.* Bettenay & Mulcahy 1972; Mulcahy *et al.* 1972) accepted the view of Woolnough (1918) and Jutson (1934) that the Meckering Line represents the landward (eastward) limit of stream rejuvenation following late Tertiary (?Pliocene) epeirogenic uplift of the Darling Peneplain to form the Darling Plateau, part of the Great Plateau of Western Australia. A very different interpretation by Finkl & Fairbridge (1979) is that the valleys west of the Meckering Line were cut by marginal uplift of the Yilgarn Craton in the Late Jurassic associated with the onset of sea-floor spreading between Australia and Greater India.

Drainage within the East Yornaning catchment is seasonal and follows a dendritic pattern in higher-order streams, which becomes rectangular in lower-order tributaries owing to the increased influence of basement structure (Fig 2). Being very close to the inland limit of incised drainage, the major valleys are still fairly flat-floored and of low gradient (Mortlock type valley form of Bettenay & Mulcahy 1972). The side-slopes of major valleys are gentle (~2.5%) and typically terminate in outcrops of fresh bedrock, or small cuestas of pisolitic duricrust, most of which dip gently to the north and are bounded by low breakaways to the south. Outcrops of pisolitic duricrust also occur as spurs extending down to the valley floors. Although the largest exposures of bedrock are in upland areas (Fig 2), fresh bedrock crops out in almost all landscape positions, including the valley floors, reflecting the highly irregular and unpredictable form of the basal weathering surface (Fig 3A). Elevation within the catchment ranges from ~310 to ~450 m AHD, with the majority of the landsurface lying between the 320 and 370 m contour intervals.

The basement rocks at East Yornaning comprise part of the Western Gneiss Terrane of the Archaean Yilgarn Craton (Myers 1990), and have been mapped by Chin (1986) as plutons of even-grained to seriate to porphyritic, biotite granites and adamellites (Fig 4A). These were emplaced after the last period of regional deformation and metamorphism, and are thus characterised by a lack of gneissic foliation or metamorphic recrystallisation. Also forming a large part of the basement in the catchment are Mesoproterozoic dolerite dykes of the Boyagin dyke swarm (Lewis 1994; Pidgeon & Nemchin 2001). The dolerite dykes are poorly exposed, but in aeromagnetic imagery can be traced for tens of kilometres across the catchment, mostly following a NW trend. In middle to upper landscape positions, the dolerite dykes are locally associated with prominent landsurface and basement highs (Fig 3A). This may be due to the relatively high resistance to weathering of the dolerite dyke itself (Bettenay *et al.* 1980), or more likely to the relatively high resistance to weathering and erosion of the baked margins in the adjoining contact metamorphosed granite (Prider 1948).

A Mediterranean climate, with cool, wet winters and hot dry summers, characterises the region. The average annual rainfall for Narrogin is about 500 mm with most rain (70%) falling during mid-May to October. Annual potential evaporation is about 1 900 mm and exceeds rainfall for 9 months of the year (Bureau of Meteorology, personal communication 1996). Most of the catchment was cleared for agriculture in the 1950s and is now widely affected by secondary salinity.

Methods

Exposures of regolith in the form of breakaways, road cuts, stream banks, drainage ditches, farm dam spoil and three transects of cored boreholes drilled to refusal depth (Fig 2) were used to produce stratigraphic sections and obtain representative samples of all major regolith rock-types (lithofacies) within the catchment. An additional 26 boreholes, drilled by the rotary air-blast method, provided more accurate information on the depth to fresh bedrock, but were not lithologically logged as part of this study. Surface exposures were mapped onto 1:25 000 scale colour aerial photographs, which in conjunction with stereoscopic observation and interpretation of airborne electromagnetic imagery (de Broekert 1996) formed the basis for the construction of a surface geology map (Fig 2).

Epoxy-impregnated thin sections were prepared of most samples to better characterise aspects of fabric, texture and composition. As a further check on mineralogical composition, samples that were thin-sectioned were also air dried, ground and X-rayed from 5–65° 2θ at 1° min^{-1} using Cu Kα radiation. Semi-quantitative estimates of mineral abundance were obtained using the SIROQUANT software package (Taylor & Clapp 1992) and kaolinite crystallinity (order–disorder) was estimated using a peak height ratio and empirical index developed by Hughes & Brown (1979).

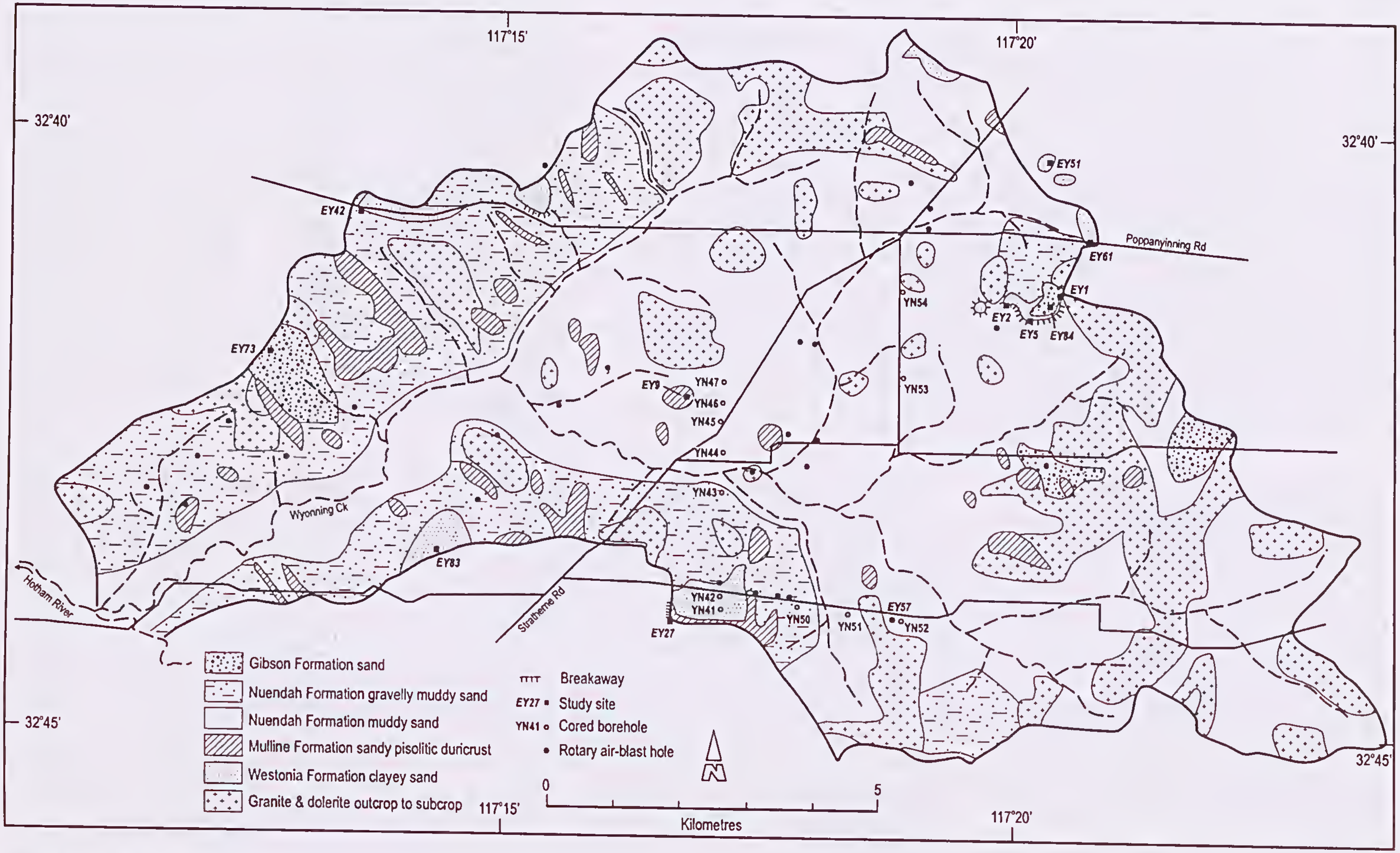

Figure 2. Geology map of the East Yornaning catchment with locations of boreholes and study sites mentioned in text.

In the course of petrographic analysis, attention was paid to differences in the textural and compositional properties of quartz (Folk 1974), this being the only primary mineral present in abundance within all lithofacies. A similar study of the varietal properties of zircon, including sensitive high-resolution ion microprobe (SHRIMP) U–Pb age determinations, is to form the subject of a separate paper.

Grain-size distributions of quartz in representative samples of each lithofacies were obtained by dry sieving at ½ ϕ intervals over the granule to fine sand-size range (4–0.063 mm, or -2–4 ϕ). Sample preparation of loose materials involved dispersion in a dilute solution of Calgon and NaOH using an overhead stirrer, followed by wet sieving through a 45 µm screen. Indurated samples, such as pisolitic duricrust, were first coarse crushed and then repeatedly boiled in concentrated NaOH and/or HCl, depending on the cementing agent. Following dissolution of the cementing minerals, the samples were disaggregated using an ultrasonic probe and then wet sieved as above. Statistical measures of the grain-size distributions (mean, mode, sorting, skewness and kurtosis) were derived by the graphic methods described by Folk (1974). Terminology of overall grain-size distribution (mud, sandy clay, gravelly sand *etc*) is based on textural triangles developed by Folk *et al.* (1970). In this classification, the term "mud" refers to a sediment composed of subequal proportions of clay-sized (<4 µm) and silt-sized (4–63 µm) particles and has no implication of moisture content. Although the textural terminology of Folk *et al.* (1970) was developed for detrital sediments, its application is here extended to some highly weathered bedrock lithofacies which are very similar in texture and mineralogical composition to certain, generally clay-rich, detrital sediments.

Stratigraphy

Weathered Granite

Distribution, geometry & dimensions. Weathered granite forms the bulk of the regolith at East Yornaning and is developed in all landscape positions except where fresh bedrock is exposed or where the Precambrian basement is composed of mafic dykes. It has a highly irregular basal surface, commonly varying greatly in thickness over small lateral distances. Nevertheless, the greatest thicknesses of weathered granite (40–50 m) tend to be concentrated along major valley floors, and along interfluve zones capped by Westonia Formation nodular sandstone or Mulline Formation pisolitic duricrust (Fig 3A).

Lithic characteristics. Based primarily on differences in overall grain-size distribution, mineralogical composition (essentially the degree to which the "weatherable" primary minerals in the parent granite have been altered) and stratigraphic position, weathered granite can be subdivided into the following three lithofacies.

1. Saprock lithofacies. This material is very similar to granite (Table 1) except for minor alteration of the chemically unstable primary minerals (*e.g.* plagioclase, biotite, hornblende, apatite) along grain boundaries, cleavage planes, cracks and other macro- and micro-structural discontinuities.
2. Lower saprolite lithofacies. This typically comprises white to yellow to light red, poorly indurated, matrix supported, coarse sandy clay (Fig 4B). Sand-sized particles are composed of muscovite, variably kaolinized microcline, and quartz, which together form a conspicuous palimpsest or remnant granitic fabric. Kaolinite pseudomorphs of biotite and plagioclase form much of the matrix and exhibit a moderate degree of crystal structure disorder.
3. Upper saprolite lithofacies. This material is typically a white, poorly indurated, coarse quartz sandy kaolinite clay, similarly exhibiting a strong remnant granitic fabric (Fig 4C). Kaolinite pseudomorphs are more prominent than in the lower saprolite facies and exhibit a moderate to low degree of disorder. Framework quartz grains are mostly strongly unimodal, coarse, poorly sorted, mesokurtic and characteristically fine to very fine skewed (Fig 5). The presence of abundant highly spherical quartz grains in the fine to very fine sand-sized sieve fractions is also characteristic (Fig 6A). Petrographic examinations of fresh granite in the catchment indicate that these occur as inclusions within alkali feldspar (Fig 6B,C) and were released from the rock following weathering of the feldspar to kaolinite (Fig 6D). Conversely, the coarse sand-sized quartz grains are all subequant, very angular, and commonly contain holes left by the weathering of inclusions, such as biotite. Polycrystalline quartz, which accounts for about half of the coarse sand-sized grains, typically comprises 3–4 roughly equally-sized crystals with strongly undulose extinction (Fig 7A,B).

A zone of unconsolidated, coarse-grained material with a highly porosity and permeability commonly occurs immediately above fresh granite and gneiss in the south-western Yilgarn Craton ("saprolite grit" aquifer of George 1990). This was not, however, observed at East Yornaning, possibly owing to poor surface exposure and the limited penetration depth of the cored boreholes.

Structure. The weathered granite lithofacies are structureless, except for where cut by dolerite dykes, faults, shear zones or quartz veins.

Stratigraphic relationships. The saprock lithofacies overlies fresh granite with a gradational contact over a vertical interval of <1 m and is overlain by the lower saprolite lithofacies with a gradational contact over a vertical interval of 1–3 m. A similarly gradational contact occurs between the lower and upper saprolite lithofacies. All three contacts are highly irregular and rapidly converge approaching outcrops of fresh granite.

Origin. Remnant granitic fabric, a progressive upward reduction in the proportion of primary minerals, gradational contacts, and the preservation of primary igneous structures, all indicate that the three lithofacies were formed by the weathering of granite. Similar materials have been described elsewhere in the south-western Yilgarn Craton by Gilkes *et al.* (1973) and McCrea *et al.* (1990), which these authors also regard as having been formed by the weathering of granite.

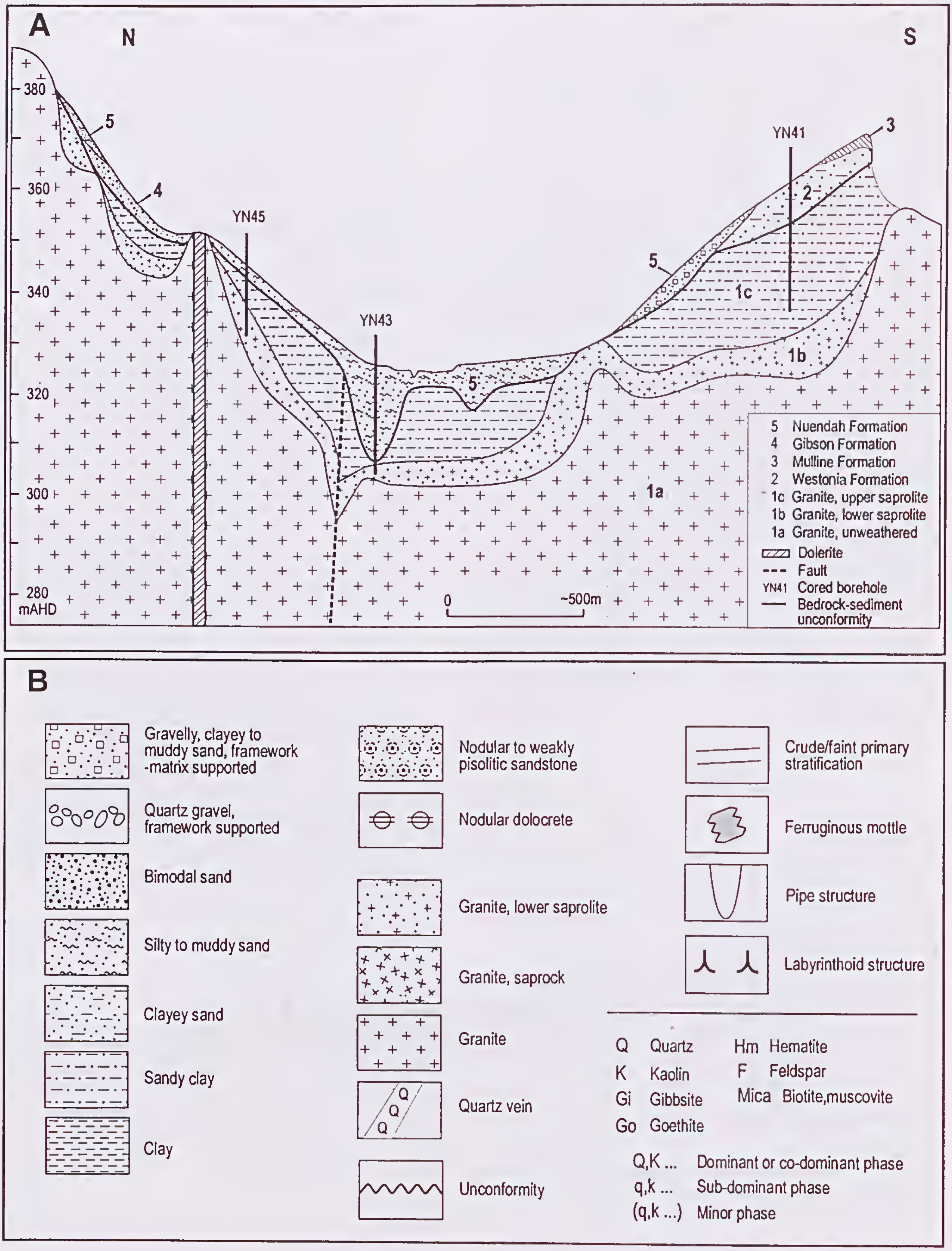

Figure 3. A: Schematic geological section across the East Yornaning catchment. Cored boreholes YN41, YN43 and YN45 positioned with respect to regolith stratigraphy rather than exact geographic location. Depths to fresh and slightly weathered basement (saprock) provided by rotary air-blast holes. B: Legend for stratigraphic sections shown in Figs 3A, 4, 8 and 10.

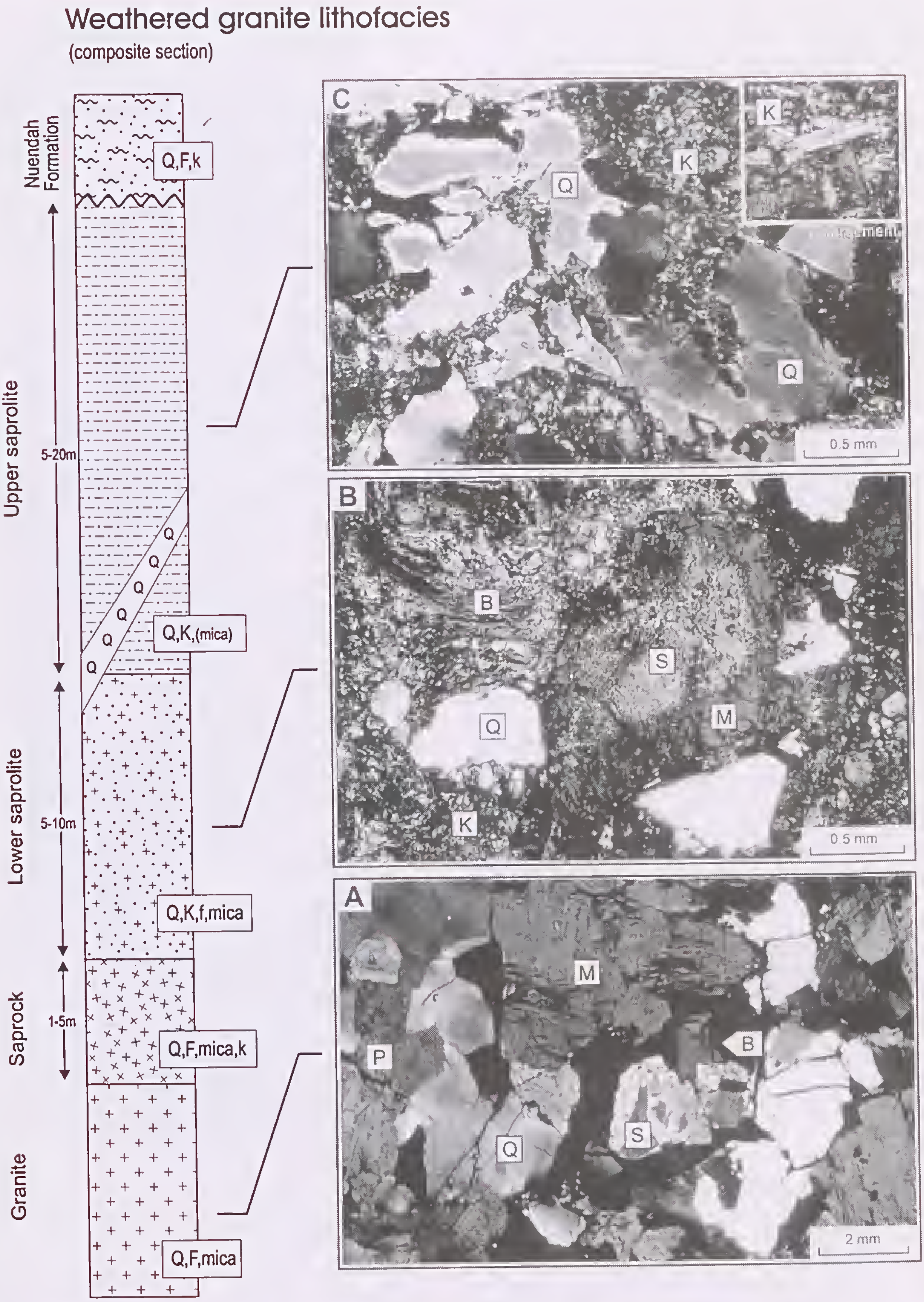

Figure 4. Composite stratigraphic section of weathered granite lithofacies with representative optical photomicrographs. A: Fresh granite. B: Lower saprolite. C: Upper saprolite. Inset in C shows enlarged view of vermiform books of kaolinite, which are optimally developed within the upper saprolite. Dominant minerals are quartz (Q), kaolin (K), biotite (B), microcline (M), plagioclase (P), and sericite (S). A = sample EY48/1, B = sample YN42 20.1 m, C = sample YN41 11.4 m; all cross-polarized light.

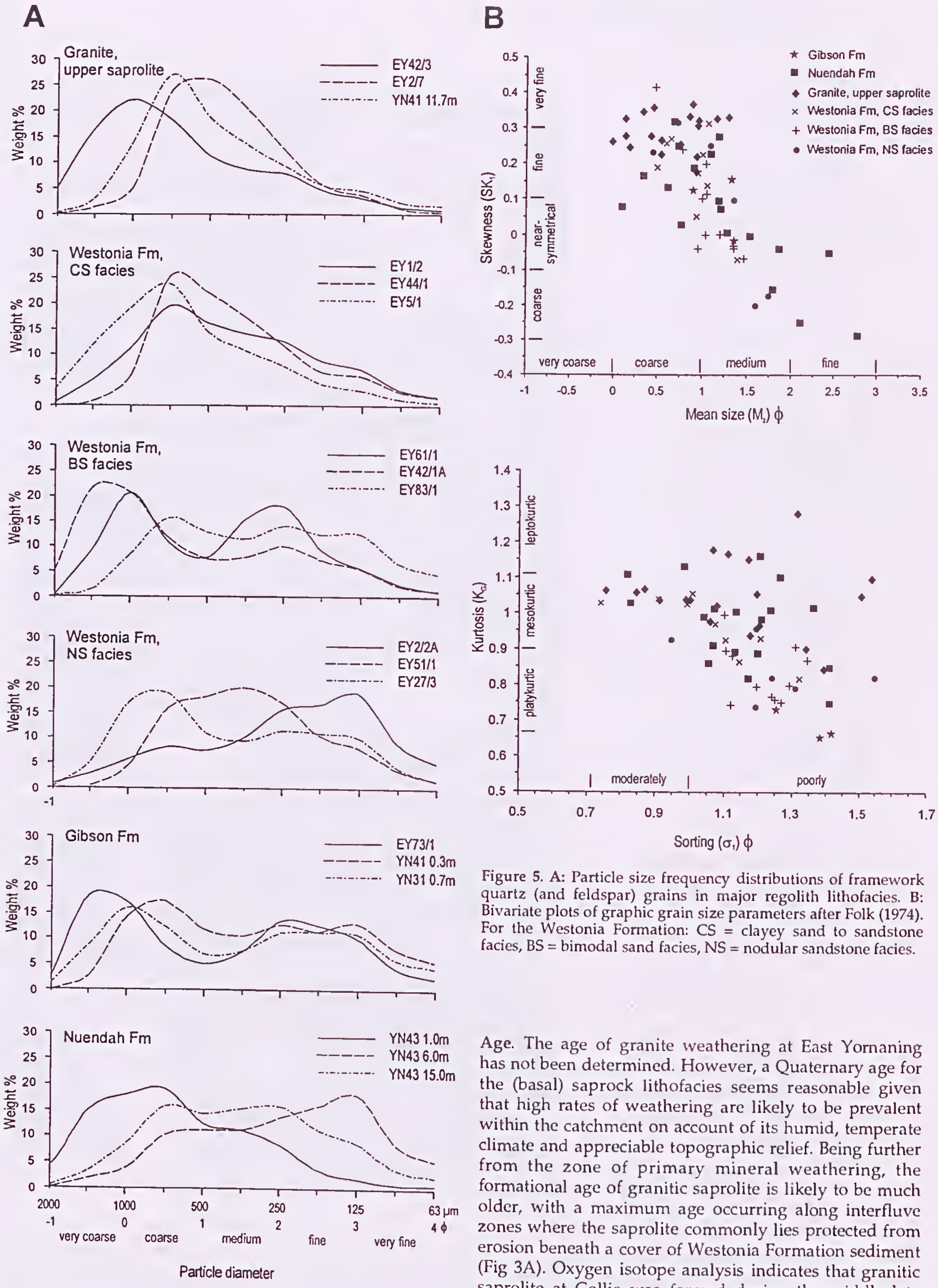

Figure 5. A: Particle size frequency distributions of framework quartz (and feldspar) grains in major regolith lithofacies. B: Bivariate plots of graphic grain size parameters after Folk (1974). For the Westonia Formation: CS = clayey sand to sandstone facies, BS = bimodal sand facies, NS = nodular sandstone facies.

Age. The age of granite weathering at East Yornaning has not been determined. However, a Quaternary age for the (basal) saprock lithofacies seems reasonable given that high rates of weathering are likely to be prevalent within the catchment on account of its humid, temperate climate and appreciable topographic relief. Being further from the zone of primary mineral weathering, the formational age of granitic saprolite is likely to be much older, with a maximum age occurring along interfluve zones where the saprolite commonly lies protected from erosion beneath a cover of Westonia Formation sediment (Fig 3A). Oxygen isotope analysis indicates that granitic saprolite at Collie was formed during the middle–late Tertiary (Bird & Chivas 1989), although a major phase of

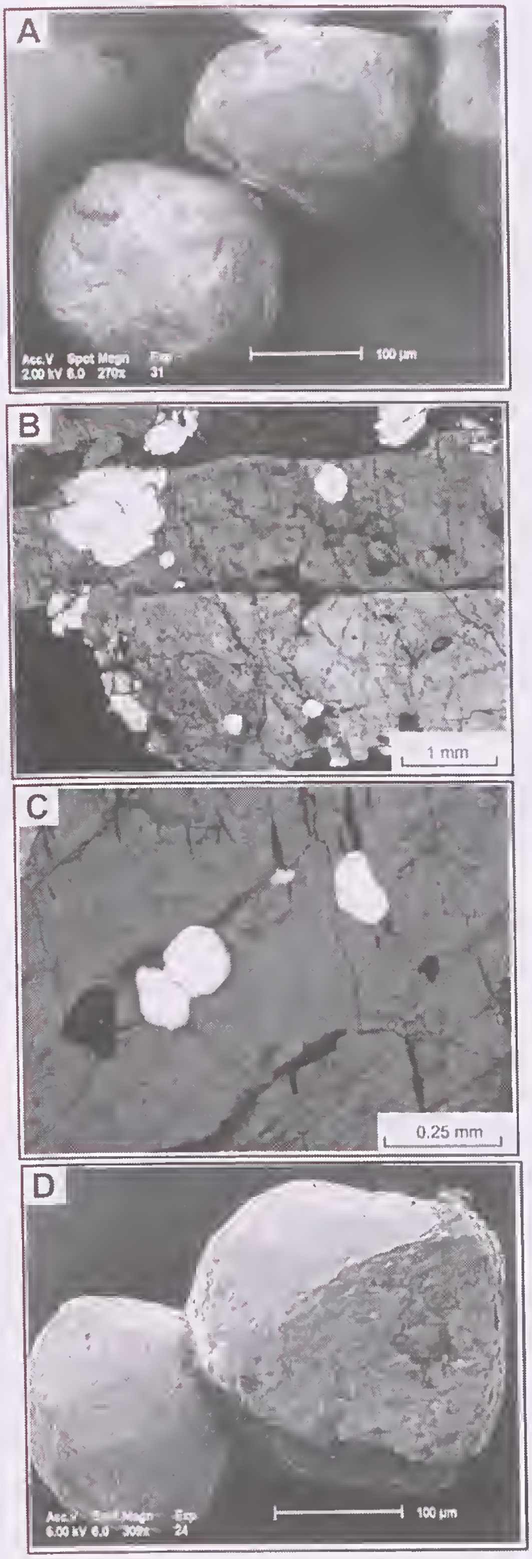

Figure 6. A: Spherical quartz grains in the fine sand-sized fraction of the Westonia Formation. B,C: Inclusions of spherical, fine to very fine sand-sized quartz in alkali feldspar within fresh granite. D: Spherical, fine sand-sized quartz grains in granitic upper saprolite after having been released from alkali feldspar by weathering. Spherical, fine sand-sized quartz grains in the Westonia Formation and other sedimentary units therefore indicative of a granitic provenance. Note that spherical grains appear "rounded", but are actually very angular when viewed under high magnifications. A = sample YN41 5.6 m, B = sample YN11/1, C = sample EY45/1, D = sample YN41 26.1 m. A,D scanning electron photomicrographs; B,C optical photomicrographs using cross-polarized light.

earliest Tertiary weathering has been identified in the eastern Yilgarn Craton based on the palaeomagnetic dating of ferruginous mottles (Pillans, in Anand & Paine 2002).

Weathered Dolerite

Distribution, geometry & dimensions. An aeromagnetic survey of the East Yornaning catchment indicates that weathered dolerite may form up to 15% of the weathered Precambrian basement (World Geoscience Corporation, unpublished data). Thicknesses of up to 40 m are common, although once again the depth of weathering is highly variable with outcrops of fresh dolerite occurring in all landscape positions. Important factors controlling the depth of weathering are likely to include dyke width and associated proximity to granitic baked margins, degree of fracturing, grain-size and mineralogical composition. Most weathered dolerite dykes are near-vertical and about 10–20 m wide (Fig 3A).

Lithic characteristics. Based on limited analyses of samples from East Yornaning and descriptions of weathered dolerite from the Darling Range (Davy 1979; Anand & Gilkes 1984), it appears that the weathering of most primary minerals in dolerite is completed over a very small vertical distance from fresh rock. The saprock and lower saprolite lithofacies are therefore very thin (1–3 m) and will not be discussed further. Upper saprolite samples of dolerite at East Yornaning typically comprise white, poorly indurated to indurated, slightly very fine quartz sandy kaolin clay. Quartz typically makes up about 5% of the rock and occurs as small (50–250 µm), angular, embayed, monocrystalline grains with slightly undulose extinction. Remnant interstitial and granophyric fabric is clearly evident in thin section.

Structure. Apart from the remnants of chilled margins and perhaps xenoliths of granitic country rock, doleritic saprolite lacks primary igneous structures. Secondary structures, in the form of thin closely-spaced ferruginous bands, very similar in appearance to Liesegang rings, are however common.

Stratigraphic relationships. The contact between weathered dolerite and weathered or fresh granite was not observed but is inferred to be vertical to subvertical, planar and sharp.

Origin and age. Remnant igneous fabric and sharp near-vertical contacts with fresh or weathered granite indicate formation by the chemical weathering of dolerite (Sadlier & Gilkes 1976; McCrea *et al.* 1990). The age of dolerite weathering would be similar to that of granite, discussed above.

Westonia Formation

Distribution, geometry & dimensions. The Westonia Formation typically occurs along major interfluve zones as tabular-shaped bodies, which are either flat-lying or gently dipping toward the valley floor (Figs 2, 3A). A maximum thickness of 9.5 m is reached in borehole YN41 (Table 1), although breakaway exposures indicate that thicknesses of 2–4 m are more typical (Table 2). The unit has been extensively truncated by erosion and may once have extended for a greater distance toward the valley floor.

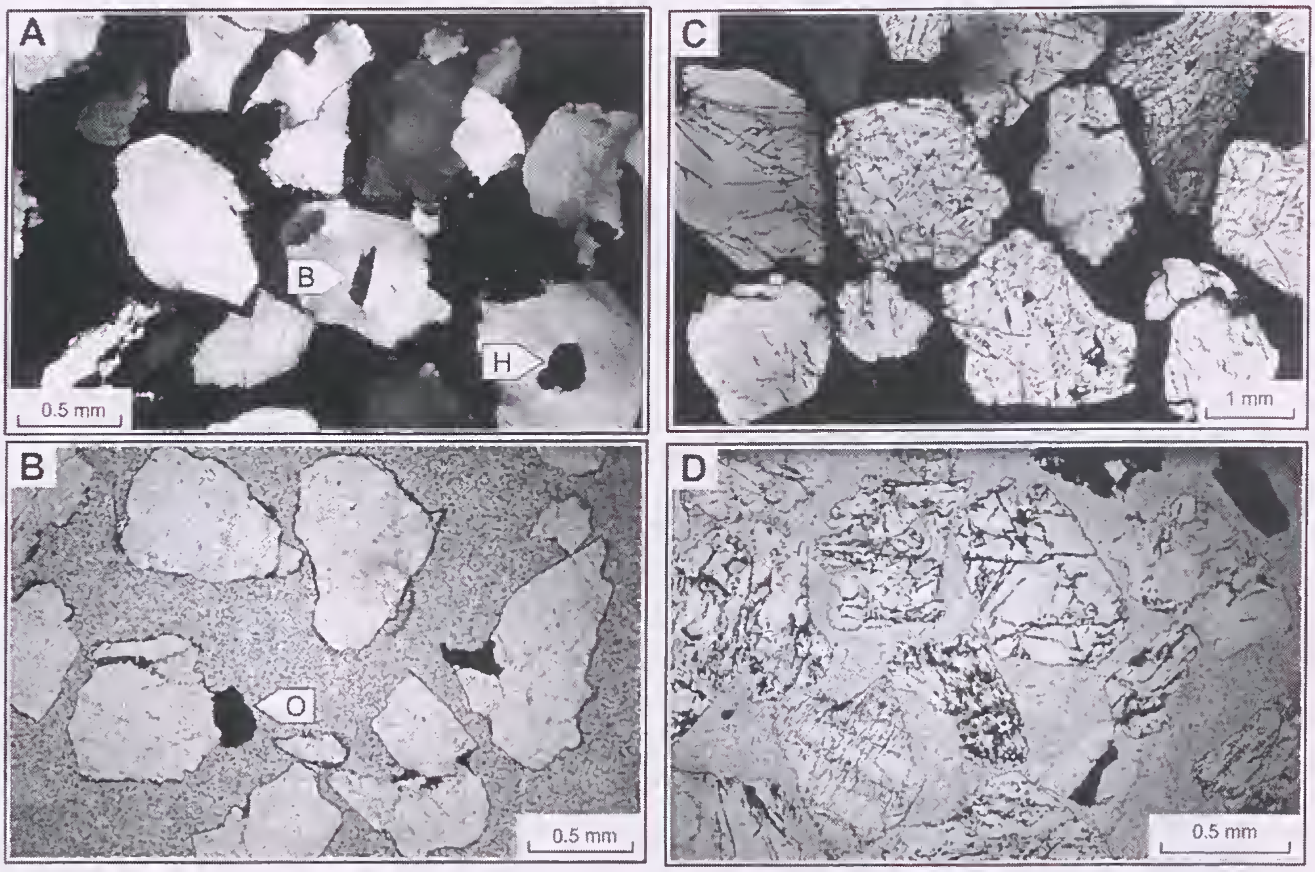

Figure 7. A,B: Optical photomicrographs of coarse sand-sized quartz grains in granitic upper saprolite. Note biotite inclusions (B), holes (H), and attachments of opaque minerals (O). C,D: Optical photomicrographs of coarse sand-sized quartz grains in the Westonia Formation. Note large proportion of fractured, etched, monocrystalline grains without holes, mineral inclusions or attachments, produced by repeated cycles of erosion, transport, deposition and alteration (weathering, pedogenesis) before being incorporated into the Westonia Formation. A,B = sample YN41 26.1 m, C = sample EY61/1, D = sample YN41 7.0 m; A,C cross-polarized light; B,D plane-polarized light.

Lithic characteristics. The Westonia Formation is subdivided into the following three major lithofacies, based primarily on differences in induration, overall grain-size distribution, quartz granulometry and the extent of nodule and pisolith development.

1. Clayey sand lithofacies. This forms the base of the Westonia Formation and is either overlain by the bimodal sand lithofacies (Table 1), or directly by the nodular sandstone lithofacies (Table 2, Fig 8A). It typically comprises yellow to light red, poorly indurated, framework to matrix supported, clayey medium to coarse quartz sand. Where exposed at the landsurface, as in the face of breakaways, the material becomes well indurated forming a clayey sandstone. Matrix (<63 µm) material is dominantly highly disordered kaolinite with lesser gibbsite, goethite and X-ray amorphous minerals. Framework quartz grains are typically unimodal, coarse, poorly sorted, mesokurtic and fine skewed (Fig 5). In contrast to granitic saprolite, the quartz grains are nearly all monocrystalline, strongly etched and free of inclusions (Fig 7C,D). Roundness within the coarser quartz grains is distinctly bimodal, comprising a primary mode of very angular to sub-angular grains and a smaller secondary mode of rounded to well-rounded grains (Fig 9A–C). The rounded quartz grains are severely pitted (Fig 9C) making them more opaque (milky coloured) than the more angular quartz grains when viewed in hand specimen.
2. Bimodal sand lithofacies. This lithofacies is only locally developed and where present crops out at the landsurface or occupies a middle position between the clayey sand and nodular sandstone lithofacies. It comprises yellow, loose to poorly indurated, framework supported, clayey bimodal coarse and fine quartz sand (Fig 5). Except for having thin coats of goethite-impregnated kaolin, the quartz grains have similar external and internal properties to the clayey sand facies. Small quantities of fine sand-sized, spherical to ovate bodies of goethitic kaolin with an internal pelletal or oolitic fabric ("kaolin spherites" of Killigrew & Glassford 1976), are also commonly present. Matrix material is dominantly highly disordered kaolinite with minor goethite and gibbsite.
3. Nodular sandstone lithofacies. This forms the uppermost part of the Westonia Formation at East Yornaning and typically comprises grey to red, well indurated, nodular to incipiently pisolitic, medium quartz sand (Fig 8B). Framework quartz grains are mostly weakly unimodal to polymodal, medium to fine, poorly sorted, platykurtic, and fine to coarse skewed (Fig 5). Rounded quartz once

Table 1

Descriptions of lithology for cored boreholes YN41, YN43 and YN45 at East Yornaning. See Fig 2 for locations.

DEPTH (m)	DESCRIPTION	ROCK UNIT
Bore YN41		
0–0.5	**Sand**; yellow, massive, loose, framework supported, bimodal coarse and fine sand, with framework particles* of poorly sorted, fine skewed quartz and kaolin spherites**; minor rounded quartz in coarser size fractions and trace microcline feldspar in finer size fractions and.	Gibson Formation
0.5–2.8	**Sandy clay**; yellow, massive, poorly indurated, matrix supported, coarse sandy clay, with framework particles of poorly sorted, fine skewed quartz and kaolin spherites in a matrix of moderately disordered kaolinitic clay, quartz, gibbsite and hematite; common yellow to red authigenic ferruginous nodules at base.	Westonia Formation
2.8–5.9	**Clayey sand**; yellow grading to white at base, massive, poorly indurated, framework supported, clayey bimodal coarse and medium sand, with framework particles of poorly sorted, near-symmetrical quartz and kaolin spherites in a matrix of highly disordered kaolinitic clay, quartz, gibbsite and hematite; common reddish brown mottles and yellow, granule-sized, spheroidal to ovate, authigenic ferruginous nodules above 5.5 m.	
5.9–9.1	**Clayey sand**; white, massive, poorly indurated, framework supported, clayey medium sand, with framework particles of moderately sorted, near-symmetrical quartz in a matrix of highly disordered kaolinitic clay, quartz and gibbsite, diffuse light red mottles at top and dark red, indurated mottles and strongly magnetic, authigenic maghemite and hematite nodules at base.	
9.1–10.1	**Sandy clay**; white, massive, poorly indurated, framework to matrix supported, coarse sandy clay, with framework particles of poorly sorted, fine skewed quartz in a matrix of slightly disordered kaolinitic clay and quartz; minor rounded quartz in coarser size fractions.	
10.1–28+	**Granitic (upper) saprolite**; white grading to yellow (goethite stained) at base, massive, poorly indurated, matrix supported, coarse sandy clay, with framework particles of moderately to poorly sorted, very fine skewed quartz in a matrix of disordered kaolinitic clay (disorder increasing with depth) and mica group minerals; quartz grains have remnant granitic fabric and kaolinite occurs a millimetre-sized vermiform books.	Archaean basement
Bore YN43		
0–2.4	**Gravelly clayey sand**; brown grading to grey at base, crudely stratified, poorly indurated, framework supported, granular clayey very coarse sand, with framework particles of moderately to poorly sorted, near-symmetrical to fine skewed quartz, feldspar (fresh) and mica in a matrix of moderately disordered kaolinitic clay and quartz; occasional rounded quartz, detrital ferruginous nodules and angular granitic rock fragments in coarser size fractions.	Nuendah Formation
2.4–17.2	**Interstratified clayey, muddy and silty sand**; grey, massive, poorly indurated, framework supported, interstratified clayey coarse sand, muddy bimodal coarse and fine sand, and silty medium to fine sand. Framework particles typically poorly sorted, near-symmetrical to coarse skewed and composed dominantly of quartz and feldspar, with feldspar decreasing in abundance and freshness with depth; occasional rounded quartz and detrital ferruginous nodules in coarser size fractions.	
17.2–17.6	**Clay**; white, massive, poorly indurated, halloysite and kaolinite clay, common sharp red mottles and authigenic ferruginous nodules.	
17.6–18.4	**Silty sand**; light grey, massive, poorly indurated, framework supported, silty very fine sand, with framework particles of moderately sorted, coarse skewed quartz.	
18.4–19.2	**Gravelly clayey sand**; light grey, massive, poorly indurated, framework supported, granular clayey coarse sand, with framework particles of poorly sorted, fine skewed quartz.	
19.2–23+	**Granitic saprock**; white grading to yellow (goethite stained) at base, massive, poorly indurated, moderately weathered, medium grained, anhedral–equigranular, aphyric, muscovite granite.	Archaean basement
Bore YN45		
1–4.2	**Gravelly muddy sand**; light grey to brown, crudely stratified, poorly indurated, framework supported, fine pebbly muddy coarse sand, with framework particles of poorly sorted, near-symmetrical to fine skewed, granule to fine pebble-sized magnetic ferruginous nodules and sand-sized quartz and feldspar (fresh) in a matrix of moderately disordered kaolinitic clay; occasional rounded quartz in coarser size fractions.	Nuendah Formation
4.2–11.0	**Granitic (upper) saprolite**; white to reddish brown, massive, poorly indurated, matrix supported, very coarse sandy clay; with framework particles of poorly sorted, fine to very fine skewed quartz and mica group minerals in a matrix of slightly disordered kaolinitic clay and goethite; quartz grains have remnant granitic fabric; slightly silicified at top.	Archaean basement
11.0–23+	**Granitic (lower) saprolite**; white to yellow; massive, poorly indurated, matrix supported very coarse sandy clay, with framework particles of poorly sorted, fine skewed quartz, feldspar (weathered) and mica group minerals in a matrix of moderately disordered kaolinitic clay; quartz grains have distinct remnant granitic fabric.	

* Framework particles are >63 mm in size; matrix particles <63 mm in size; ** framework particle types listed in decreasing order of abundance.

Table 2

Descriptions of lithology for breakaway exposure EY2 at East Yornaning. Note that Gibson Formation sand occurs ~50 m back from breakaway face. See Fig 2 for location.

DEPTH (m)	DESCRIPTION	ROCK UNIT
0–0.3	**Sand**; light grey, loose, framework supported, bimodal coarse and fine sand, with framework particles* of poorly sorted, near-symmetrical quartz**; trace microcline feldspar in finer size fractions and trace rounded quartz in coarser size fractions.	Gibson Formation
0.3–0.5	**Nodular clayey sand**; as above, except cemented into large, highly irregular, light red nodules by fine sand- to silt-sized quartz, kaolinitic clay, goethite and hematite.	
0.5–0.8	**Nodular to weakly pisolitic sandstone**; reddish yellow, nodular to weakly pisolitic, indurated to well indurated, framework supported, weakly bimodal medium and coarse sand, with framework particles of poorly sorted, coarse skewed quartz in a matrix of gibbsite, silt-sized quartz, highly disordered kaolinitic clay and goethite; minor rounded quartz in coarser size fractions; numerous voids between nodules and incipient pisoliths.	Westonia Formation
0.8–2.1	**Clayey sandstone**; reddish yellow, crudely horizontally stratified, indurated to well indurated, weakly silica cemented; framework to matrix supported, clayey coarse sand, with framework particles of poorly sorted, near-symmetrical quartz in a matrix of highly disordered kaolinitic clay, gibbsite and goethite; minor rounded quartz in coarser size fractions and scattered angular pebbles of vein quartz at base.	
2.1+	**Granitic (upper) saprolite**; white, massive, poorly indurated, matrix supported, coarse sandy clay, with framework particles of moderately sorted, fine skewed quartz, in a matrix of kaolinitic clay and mica group minerals.	Archaean basement

* Framework particles are >63 mm in size; matrix particles <63 mm in size; ** framework particle types listed in decreasing order of abundance.

again forms a minor but conspicuous part of the coarse to very-coarse sand sized fraction. Matrix material is dominantly silt-sized quartz, gibbsite, goethite, hematite and highly disordered kaolinite.

Structure. The clayey sand to sandstone facies is crudely horizontally stratified, very similar to near-modern deposits of Nuendah Formation muddy sand, which occupy the same valley-side and interfluve landscape positions (Fig 3A). The other facies lack primary sedimentary structures, but commonly contain pipes outlined by hematitic mottles and infilled with similar material to the sediment in which they occur. Similar structures are widespread at the Jarrahdale bauxite deposit and have been interpreted by Grubb (1966) to be infilled cavities left by the decay of ancient plant roots.

Stratigraphic relationships. The Westonia Formation typically unconformably overlies weathered Precambrian granite and dolerite with a sharp contact. Where not exposed at the landsurface, it is typically unconformably overlain by the Gibson Formation with a sharp contact, or the Mulline Formation with a gradational contact over a vertical interval of about 0.2 m.

Correlation. In terms of lithology, stratigraphic position and landscape position, the three lithofacies of the Westonia Formation at East Yornaning correlate most closely with the sandstone to muddy sandstone facies of the Westonia Formation as defined by Glassford (1987). A similarity in terms of lithology, stratigraphic and landscape position also exists with the ?Eocene Kojonup Sandstone (Churchill, in McWhae *et al.* 1958), although this sediment contains plant macrofossils, a basal conglomerate, and is partly feldspathic (Wilde & Backhouse 1977), which is unlike the Westonia Formation at East Yornaning or its type section.

The Quagering Beds of Finkl & Fairbridge (1979) is an angular quartz sand with rounded quartz pebbles which is underlain by Precambrian basement, overlain by "laterite", and distributed as "upland residuals" along the Ravensthorpe Ramp south of Bridgetown. As such, it too may be a lithostratigraphic equivalent of the Westonia Formation.

Origin. Crude primary sedimentary structures, bimodal grain-size distributions and rounded quartz grains all indicate that the Westonia Formation is sedimentary and was not produced by the *in situ* chemical weathering of granite. Furthermore, the Westonia Formation overlies dolerite dykes from which, given the large differences in quartz abundance and grain-size, it cannot have been produced by *in situ* weathering.

Close similarities in terms of landscape position, geometry, structure and overall grain-size distribution between the clayey sand facies of the Westonia Formation and the muddy sand facies of the Nuendah Formation, suggest that the two units share a common origin, albeit widely separated in time. Since the Nuendah Formation ranges to the present and is currently forming along valley sides by a combination of unconfined sheet-wash and downslope creep (see below), it can be inferred that the basal clayey sand facies of the Westonia Formation formed in a similar manner.

The combination of well-developed grain-size bimodality, kaolin spherites and clay-coated quartz grains within the bimodal sand facies of the Westonia Formation is suggestive of an aeolian origin (Folk 1968; Warren 1972; Glassford & Semeniuk 1995). Such an interpretation is also consistent with the lithofacies' patchy distribution and valley side position, with all aeolian cross-stratification having been destroyed by bioturbation (root growth, faunal burrowing *etc*) and the clayey matrix having been produced by the post-

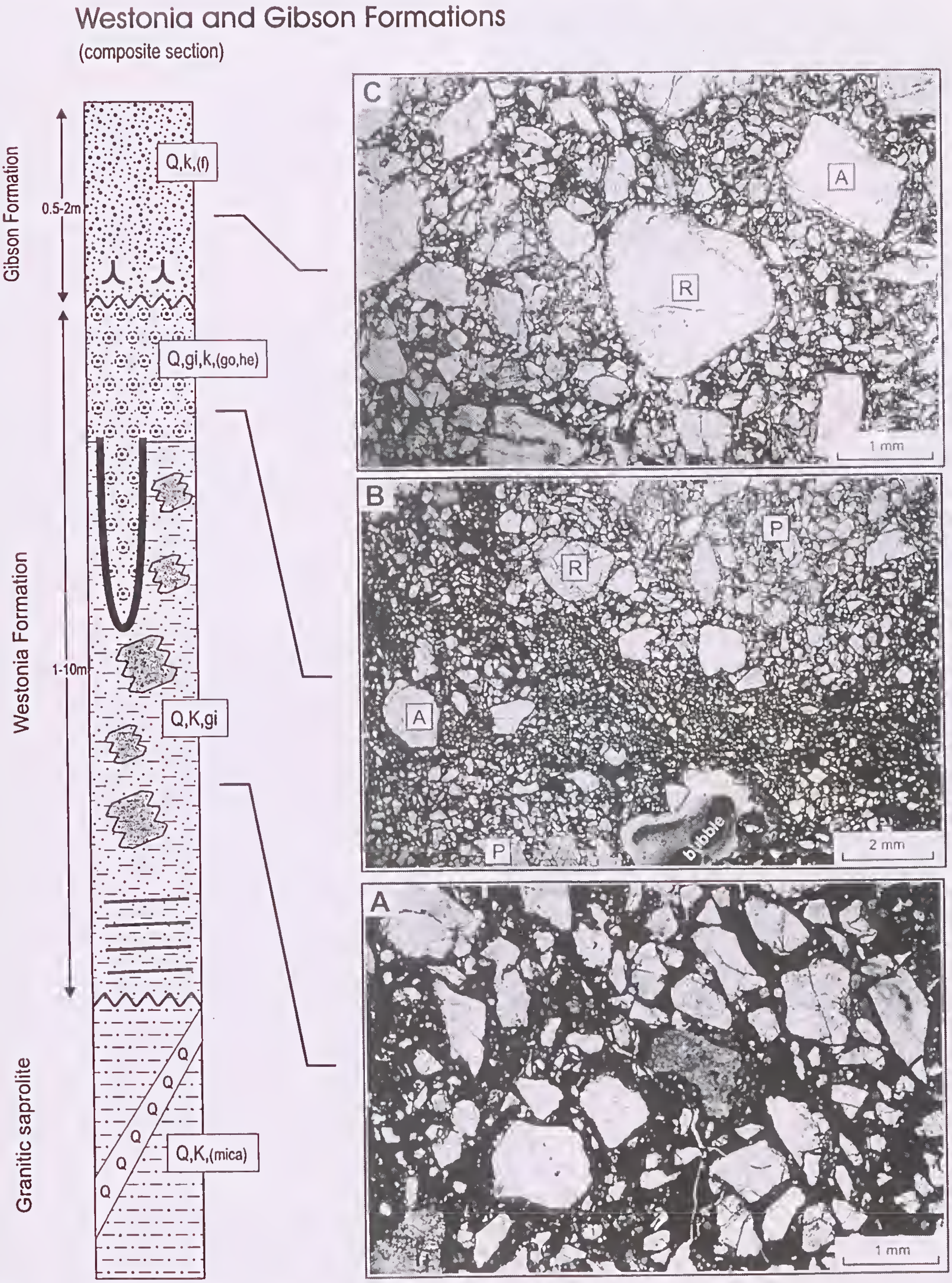

Figure 8. Composite stratigraphic section of the Westonia and Gibson formations with representative optical photomicrographs. **A:** Westonia Formation clayey sandstone. **B:** Westonia Formation nodular sandstone. **C:** Gibson Formation grey bimodal sand. Note incipient pisolith nuclei (P) in Westonia Formation nodular sandstone, and combination of well rounded to rounded (R) and very angular to subangular (A) quartz grains in Westonia Formation nodular sandstone and Gibson Formation grey sand. A = sample EY2/1C, B = sample EY2/2, C = sample EY65/1; all plane-polarized light.

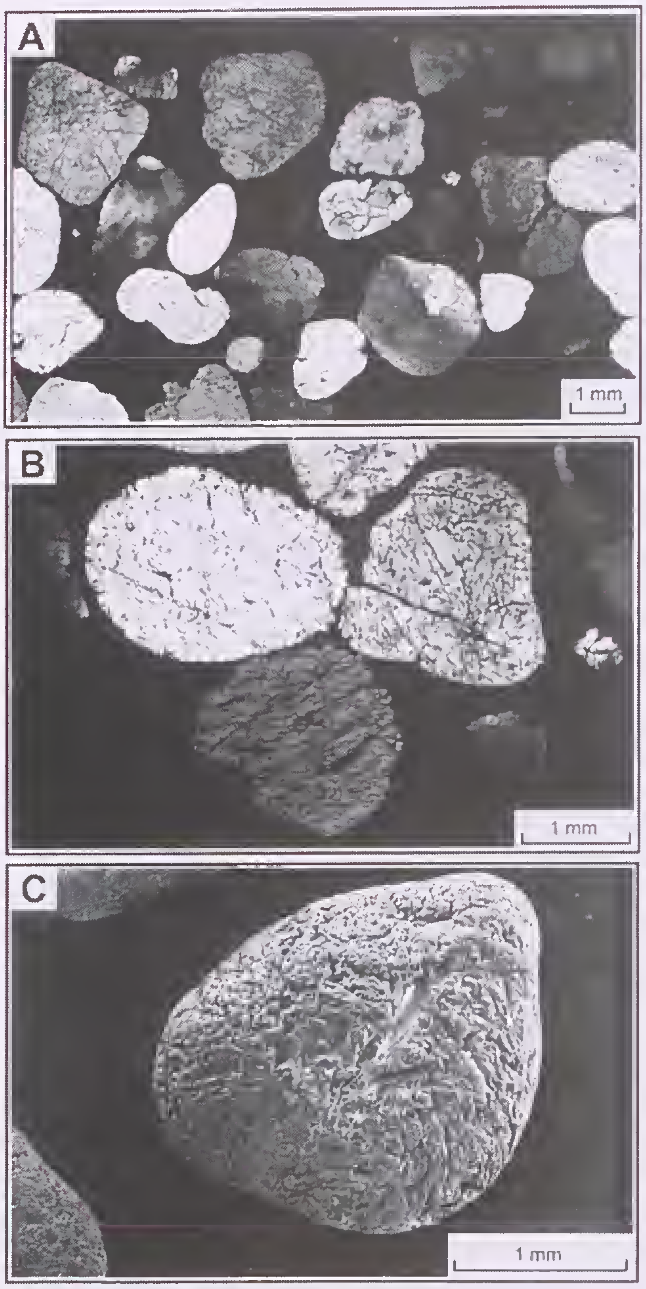

Figure 9. A–C: Rounded, very coarse sand-sized quartz grains in the Westonia Formation. The rounded quartz grains were probably ultimately sourced from an ancient texturally mature (?fluviatile) sediment. A,B = sample EY61/1 optical photomicrographs cross-polarized light. C = sample EY61/1 scanning electron photomicrograph.

depositional infiltration of fine particles, possibly derived from aeolian dust.

Post-depositional infiltration of fine material seems to have played a much more prominent role in development of the nodular sandstone facies of the Westonia Formation. In this case, large quantities of very fine to fine sand-sized quartz appear to have penetrated the uppermost part of the bimodal sand facies, or more commonly the clayey sand to sandstone facies (Table 2). Accompanying or following the influx of fine material, there has been a segregation of coarser and finer quartz grains to form nodules, which, with further reorganization become incipiently pisolitic. Good examples of this progression are shown in Fig 8B and Plate 1A.

Comparisons between thin sections and grain-size distributions show that the degree to which nodules are developed is directly proportional to the amount of fine sand added by infiltration. Thus, samples with a quartz grain-size distribution similar to that of the original clayey sand sediment, such as EY27/3 in Fig 5A, are only weakly nodular. Samples, such as EY2/2A, in which a fine mode and negative skew have been created by the addition of abundant fines, are on the other hand strongly nodular. Confinement of this process to the uppermost metre or so of the Westonia Formation only and the absence of broken rounded quartz grains (Fig 8B) indicates that the "addition of fines" is not simply a result of *in situ* quartz particle breakage associated with weathering or pedogenesis.

Provenance. Possible sources of the fines in the nodular sandstone facies of the Westonia Formation include (1) aeolian dust, as in the case of the bimodal sand facies of the Westonia Formation, (2) the overlying Gibson Formation, which also comprises a large proportion of fine to very fine sand-sized quartz (Fig 8C), and (3) some other overlying sediment, all vestige of which was removed during creation of the unconformity that separates the Westonia and Gibson formations.

Weathered granite is likely to have been the dominant source-rock for the other two Westonia Formation lithofacies, although the reworking of a pre-existing texturally mature (?fluviatile) sedimentary cover is indicated by the presence of small quantities of well-rounded quartz grains. The preponderance of monocrystalline quartz grains, both rounded and angular, with numerous embayments and etch features, variously filled with matrix material (Fig 7C,D), further suggests that both source-rock types had been subjected to pedogenesis (Cleary & Conolly 1972; Eswaran *et al.* 1975). An abrupt change to much fresher quartz grains in granitic saprolite immediately below the Westonia Formation (Fig 7A,B) indicates that pedogenic alteration of the quartz grains was not primarily achieved after deposition of the Westonia Formation.

Age. There is no evidence that can be used to directly date deposition of the Westonia Formation. However, since the unit is extensively eroded and unconformably overlain by the Gibson Formation, interpreted to be Pleistocene, a middle–late Tertiary age seems likely. This concurs with a probable Eocene age for the Kojanup Sandstone (Wilde & Backhouse 1977) and Quagering Beds (Finkl & Fairbridge 1979).

Mulline Formation

Distribution, geometry & dimensions. As with the Westonia Formation, the Mulline Formation comprises only a small proportion of the regolith at East Yornaning. It forms small, dissected plateaux ("lateritic gravel plains") along interfluve zones and small rounded hills in various landscape positions. Less commonly, it occurs as narrow discontinuous spurs that extend for several hundred metres from the interfluve zones toward the valley floors (Fig 2). The consistent

NW trend of these suggests a close genetic relationship with dolerite dykes or the baked margins in granite alongside the dolerite dykes. The small hills capped by Mulline Formation are, on the other hand, mostly composed of variably weathered granite, whereas the interfluve plateaux are mostly composed of the Westonia Formation. Although rarely fully exposed, it appears that the Mulline Formation has an undulating sheet-like geometry with an average thickness of about one metre.

Lithic characteristics. The Mulline Formation is typically a reddish brown, indurated to well indurated, strongly nodular to pisolitic, quartz sandy aluminous duricrust (Plate 1B). Pisoliths range up to about 1.5 cm in diameter and comprise nuclei of framework- to matrix-supported fine to coarse quartz sand, enveloped by laminae of framework-supported fine to very fine quartz sand. Contacts between laminae are commonly disconformable suggesting multiple phases of growth by accretion. The inter-pisolith domain typically comprises pisolith fragments and quartz sand thickly coated by gibbsite, which also commonly occurs as ooids. Matrix material of the pisolith nuclei, their surrounding laminae and the inter-pisolith domain is fine-grained gibbsite, quartz, X-ray amorphous minerals, highly disordered kaolinite, hematite, maghemite and boehmite, in approximately that order of decreasing abundance.

Two less common, but highly genetically significant, variations occur with respect to the composition of the pisolith nuclei. The first relates to Mulline Formation duricrust overlying dolerite, wherein the pisolith nuclei tend to be very iron-rich and contain only a few small highly corroded quartz grains. The second relates to where Mulline Formation duricrust directly overlies weathered granite, wherein the pisolith nuclei exhibit a well-developed remnant granitic fabric in which the remnants of quartz–feldspar–mica domains can be recognised.

Differentiation of the three types of Mulline Formation is generally difficult to achieve in the field, hence separate lithofacies have not been established. Nevertheless, there is a tendency for those pisoliths with remnant granitic nuclei to be loosely packed, large and irregularly shaped (more nodular than pisolitic). Pisoliths with highly ferruginous nuclei situated over dolerite tend to be equally large and poorly formed, but in this instance much more dense, magnetic and dark red.

Structure. The Mulline Formation is typically massive, but sporadically contains cavities and vertical pipes that are empty to partly filled with detritus. As with the nodular sandstone facies of the Westonia Formation, the pipes are probably related to the growth and decay of ancient plant roots.

Stratigraphic relationships. The basal surface of the Mulline Formation is poorly exposed, but is inferred to be gradational with weathered granite, weathered dolerite and thick sequences of Westonia Formation.

Correlation. Except for a lack of kaolin spherites and a greater abundance of secondary aluminium minerals (principally gibbsite), the Mulline Formation at East Yornaning is very similar to the Mulline Formation at its type section (Glassford 1987). It also correlates in terms of lithology and stratigraphic position with most other pisolitic iron- and aluminium-rich duricrusts in the south-western Yilgarn Craton (*e.g.* Mulcahy 1967; Finkl & Churchward 1973; Hickman *et al.* 1992), although these may not all have been formed by the same process or at the same time.

Origin. Mulline Formation pisolitic duricrust is essentially a secondary or "overprint" lithofacies that cuts across primary lithological contacts. In some cases it has developed entirely within sediment (Westonia Formation), whereas in others it has developed within weathered Precambrian granite or dolerite. The nature of the original or "host" material is most clearly reflected by the composition of the pisolith nuclei, rich in quartz sand rich for Westonia Formation, hematite-rich for weathered dolerite, and gibbsite-rich (with remnant granitic fabric) for weathered granite. In the case of weathered granite, it is necessary for the host material to have been either saprock or lower saprolite in order to account for the presence of gibbsite pseudomorphs after feldspar within the pisolith nuclei.

The alteration (pedogenetic, diagenetic, weathering) processes responsible for ferruginous or aluminous pisolitic duricrust formation are complex, varied and beyond the scope of this paper (*e.g.* Nahon 1991; Anand & Paine 2002). An essential ingredient in the formation of Mulline Formation pisolitic duricrust, however, appears to have been the addition of fine to very fine quartz sand (Glassford & Semeniuk 1995), in the same manner inferred to be responsible for development of the nodular sandstone facies of the Westonia Formation. Indeed, the nodular sandstone facies of the Westonia Formation can be regarded as an immature form of, or transition to, the sand-rich facies of the Mulline Formation (compare Plates 1A and 1B). Incipiently developed pisoliths within some samples of otherwise strongly pisolitic sand-rich Mulline Formation, provide further evidence of this paragenetic sequence.

Another condition necessary for the development of Mulline Formation pisolitic duricrust appears to have been a fairly impermeable substrate, preventing excessive downward movement and dilution of the added fine sand grains (Glassford & Semeniuk 1995). This requirement would have been readily satisfied in the case of outcropping weathered basement and thin successions of Westonia Formation overlying weathered basement, but would not have been achieved where the Westonia Formation was thick. Thus, depending on its thickness, the Westonia Formation may either have been completely converted to Mulline Formation, or incompletely transformed to Mulline Formation over a small depth beneath the ancient landsurface (Table 2).

Age. The age of Mulline Formation pisolitic duricrust has not been directly determined. However, a late Tertiary (?Miocene) age seems probable based on an inferred middle to late Tertiary age for the Westonia Formation, which it overprints, and an inferred Quaternary age for the Nuendah Formation, into which the Mulline Formation has been reworked. Using palaeomagnetic evidence, a late Tertiary age for "lateritization" has also been determined by Schmidt & Embleton (1976) for outcrops of Paleozoic and Mesozoic sediments in the northern Perth Basin (data reinterpreted by Pillans, in Anand & Paine 2002).

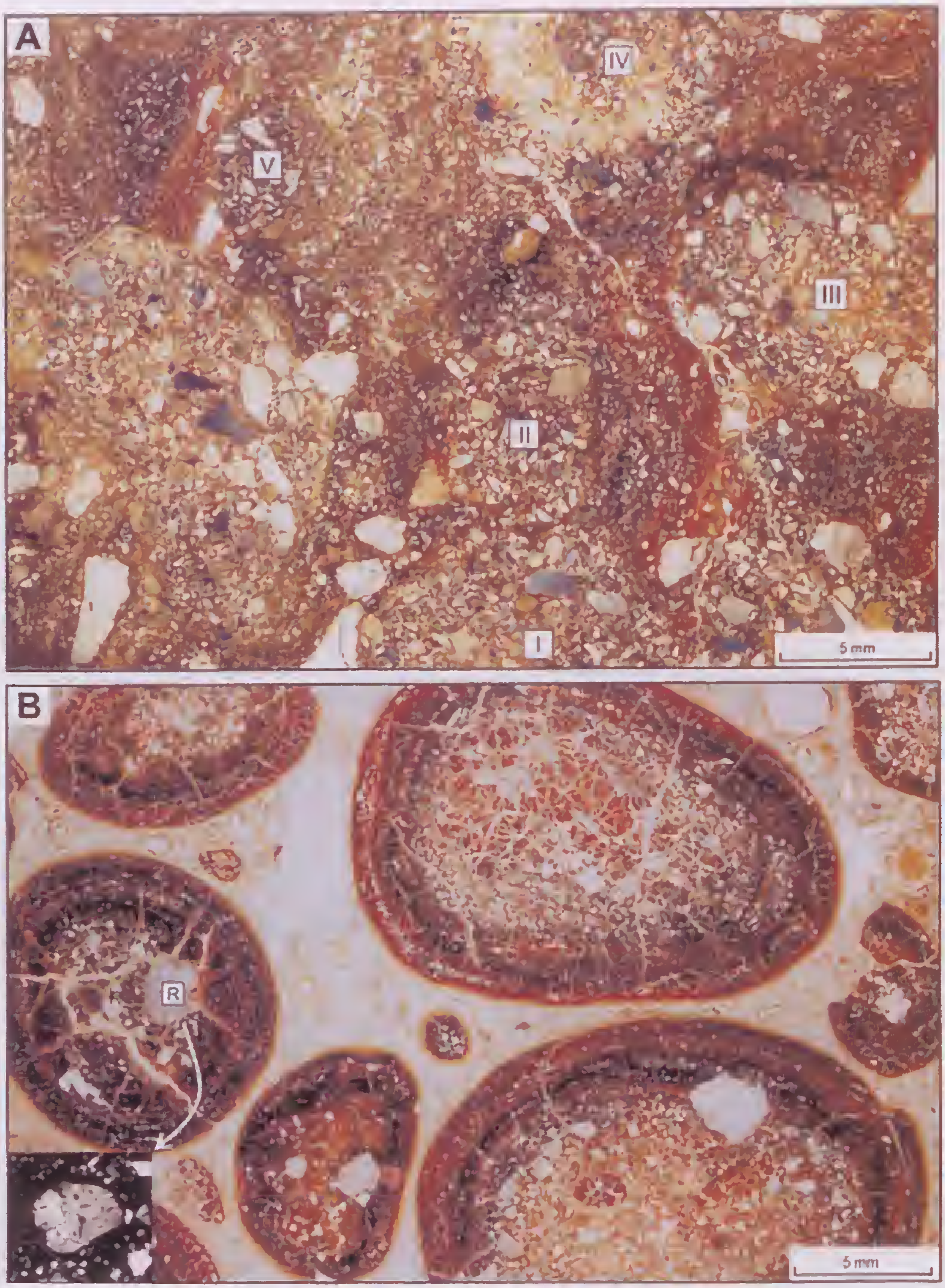

Plate 1. A: Nodular sandstone facies of the Westonia Formation showing development of nodules and incipient pisoliths (numbered I–V), transitional to Mulline Formation sandy pisolitic duricrust (see photomicrograph below). Nodule and incipient pisolith nuclei are composed of coarser quartz grains typical of underlying clayey sand facies of the Westonia Formation, whereas the intervening areas are composed of allogenic finer quartz grains arranged into poorly- to well-developed curvilinear laminae around the nuclei. **B:** Mulline Formation sandy pisolitic duricrust developed within the upper part of the Westonia Formation. Inset shows enlarged and rotated view of a corroded well-rounded quartz grain (R) in one of the pisolith nuclei. A = sample EY2/2A, B = sample EY 9/1. A,B plane polarised light, inset in B cross-polarised light.

Gibson Formation

Distribution, geometry & dimensions. At East Yornaning, the Gibson Formation occurs as small sheets and pods situated in middle to upper slope positions (Fig 2). A marked increase in abundance of the Gibson Formation east of the Meckering Line (Brewer & Bettenay 1973; Glassford 1987), where the climate becomes drier and there has been less fluvial reworking of surficial material, suggests that the sheets of Gibson Formation at East Yornaning were once much more extensive. Limited borehole intersections and sand pit exposures (Tables 1, 2) indicate that the Gibson Formation has a thickness of 0.5–2 m.

Lithic characteristics. The following two lithofacies of the Gibson Formation can be recognised, based primarily on differences in colour.

1. Grey bimodal sand lithofacies. This facies forms the vast bulk of the Gibson Formation at East Yornaning and is composed of white to light grey, loose to poorly indurated, framework supported, poorly sorted, bimodal very coarse and fine quartz sand (Fig 5). Trace amounts of fresh microcline feldspar can be detected in X-ray diffractograms and thin sections of the medium to fine sand-sized sieve fractions. Framework quartz grains are virtually all monocrystalline, highly etched and very angular to angular, though a small proportion of coarse, well rounded to rounded quartz is also present (Fig 8C). Where overlying granitic saprolite, or some other impermeable material, basal sections of Gibson Formation grey sand contain large, irregularly-shaped, authigenic ferruginous nodules (Table 2), or less commonly a ~0.5 m thick zone cemented by kaolin, gibbsite, goethite and silt-sized quartz (Fig 8).
2. Yellow bimodal sand facies. This facies has a very restricted spatial distribution at East Yornaning, having only been found in the top of borehole YN41 (Table 1). The yellow sand facies of the Gibson Formation is very similar in composition and texture to the grey bimodal sand facies, except that it contains a high abundance of kaolin spherites (~10% in YN41) and has framework quartz grains with thin coats of yellow, goethite-impregnated, kaolinitic clay. The yellow bimodal sand facies of the Gibson Formation can be distinguished from the bimodal sand facies of the Westonia Formation, which is also yellow, on the basis of stratigraphic position and by the presence of trace quantities of fresh feldspar and a larger amount of kaolin spherites.

Structure. Except for authigenic ferruginous nodules, and labyrinthoid structures developed within the basal cemented zone of the grey sand lithofacies (Fig 8), the Gibson Formation is massive.

Stratigraphic relationships. Gibson Formation bimodal sand unconformably overlies the Westonia Formation and variably weathered Precambrian granite and dolerite with a sharp contact (Tables 1, 2). It also unconformably overlies Mulline Formation pisolitic duricrust, but in this case the contact is highly irregular owing to the infilling of cavities with the upper part of the duricrust. Where not exposed at the land surface, the Gibson Formation is unconformably overlain by the Nuendah Formation. An interfingering contact between the Gibson and Nuendah formations is, however, locally present in he central and north-eastern parts of the Yilgarn Craton (Glassford 1987; Glassford & Semeniuk 1995), indicating that the two formations are at least in part temporally equivalent. The presence of an interfingering contact could not be confirmed at East Yornaning due to the lack of suitably positioned boreholes and exposures.

Correlation. Both grey and yellow bimodal sand lithofacies of the Gibson Formation at East Yornaning correlate in terms of geometry, lithology and stratigraphic position with the sand sheet faces of the Gibson Formation in the central and north-eastern Yilgarn Craton (Glassford 1987). A major difference, however, is that the Gibson Formation at East Yornaning is dominantly grey, whereas the Gibson Formation in central and eastern parts of the Yilgarn Craton is dominantly yellow or reddish yellow (Glassford 1987).

Yellow and grey sands with or without coarse sand- to pebble-sized rounded quartz particles are also widely distributed in upland positions along the south-western margin of the Yilgarn Craton (Mulcahy 1960; Mulcahy *et al.* 1972; Finkl & Fairbridge 1979; Bettenay *et al.* 1980; Asumadu *et al.* 1991). In the Darling Range, these sands occupy shallow troughs along major interfluve zones (Goonaping valley form of Bettenay & Mulcahy 1972) and are locally cemented to form a thin "duricrust" (Bettenay *et al.* 1980; Asumadu *et al.* 1991). In both of these respects, this sediment is similar to the Gibson Formation at East Yornaning.

Origin. Basal contacts with a variety of regolith strata, including weathered dolerite dykes, and the presence of a small but distinct quantity of well rounded quartz grains, indicate that the Gibson Formation is sedimentary, and not derived from the *in situ* weathering of Precambrian crystalline basement. Well-developed bimodal grain-size distributions, the presence of kaolin spherites in the yellow sand facies, and a widespread distribution throughout all landscape positions, including the interfluve zones between major drainage basins, further indicate that the Gibson Formation is likely to be aeolian (Glassford & Semeniuk 1995).

The gradation between yellow sand in eastern (drier) areas and grey sand in western (wetter) areas indicates that the grey sand was formed from the yellow sand by the degradation of kaolin spherites and removal of goethitic clay coatings from quartz grains as a consequence of increased rainfall and water throughflow. Assisting in the removal of grain coatings and bleaching of the yellow quartz sand is likely to have been the complexing and mobilization of iron by organic exudates (Hingston 1963; Enright 1978).

Basal cementation of the grey sand facies of the Gibson Formation probably resulted from the downward translocation of silt-clay sized material derived from the degradation of kaolin spherites and the removal of grain coatings from originally yellow sand, as noted above. Additional silt-clay sized particles would have been derived from matrix material deposited along with the framework grains or thereafter, such as from aeolian dust.

Provenance. Trace quantities of fresh microcline feldspar within the Gibson Formation indicate that it was partly derived from exposures of fresh granite, although outcrops of granitic saprolite and the Westonia and Mulline formations are also likely to have been important sources. Aeolian dust, infiltrated into the bimodal sand during or after its deposition, is likely to have been sourced from outside of the drainage basin.

Age. On the basis of its inferred aeolian mode of deposition and uppermost stratigraphic position, the Gibson Formation is likely to have been deposited during arid phases coeval with high latitude glaciations during the Pleistocene (Glassford & Semeniuk 1990, 1995). Bleaching and fluvial reworking of the originally mainly yellow quartz sand is likely to have been accomplished during the Holocene, or interglacial phases during the Pleistocene when the climate would have been relatively humid and a relatively thick vegetation cover would have been supported.

Nuendah Formation

Distribution, geometry & dimensions. The Nuendah Formation forms most of the landsurface at East Yornaning (Fig 2) and comprises the bulk of the sedimentary regolith volume. It occupies narrow palaeovalleys cut into weathered basement beneath the modern valley floors and extends up the valley sides as irregular sheets that wedge out against outcrops of fresh granite, or less commonly, outcrops of the Westonia and Mulline formations (Fig 3A). A thickness of about 20 m for the Nuendah Formation appears to be typical where it fills palaeovalleys, decreasing to an average of about 2 m where it mantles the valley sides.

Lithic characteristics. The Nuendah Formation is very lithologically heterogeneous, but can be broadly subdivided into the following two major lithofacies based on differences in overall grain-size distribution and mineralogical composition.

1. Muddy sand lithofacies. This facies dominates the valley floors throughout the catchment, and also the valley sides in the upper (eastern) part of the catchment where outcrops of granite are particularly widespread. Typically, it comprises light grey, poorly indurated, framework supported, muddy to clayey, medium to coarse sand (Fig 10B,C). Framework grains are weakly unimodal to polymodal, poorly sorted, mesokurtic to platykurtic, coarse to fine skewed (Fig 5), and composed of angular mono- and polycrystalline quartz, granitic rock fragments, and microcline and plagioclase feldspar (Fig 10B,C). Where filling palaeovalleys, there is an overall decrease in the abundance of feldspar and granitic rock fragments with depth. Matrix material typically comprises silt-sized quartz and feldspar, and moderately disordered kaolinite.
2. Gravelly muddy sand lithofacies. This facies dominates interfluve zones and upper valley slopes in the lower (western) part of the catchment, where outcrops of Mulline Formation pisolitic duricrust and Westonia Formation nodular sandstone are most common (Fig 2). It interfingers downslope with the muddy sand facies, and typically comprises grey to brown, poorly indurated, framework supported, gravelly muddy sand (Fig 10A). Gravel particles range from granule to coarse pebble in size and are composed of feldspar, granitic rock fragments, and brown ferruginous nodules and pisoliths with chipped and polished external surfaces. Matrix muddy sand is of similar texture and composition to the muddy sand facies, described above.

Structure. The muddy sand facies is crudely horizontally stratified along valley sides and normally-graded in ephemeral stream channels. Interbedding of the two Nuendah Formation lithofacies is widespread in lower slope and valley floor positions.

Stratigraphic relationships. In valley floor and side positions, the Nuendah Formation typically unconformably overlies the upper saprolite facies of weathered granite with a sharp contact. However, where filling palaeovalleys, it unconformably overlies the saprock facies of weathered granite with a sharp contact marked by a thin angular quartz gravel lag (Table 1; Fig 10). Less commonly, the Nuendah Formation unconformably overlies the Gibson Formation with a sharp contact. Lithostratigraphic investigations of regolith in the central and north-eastern Yilgarn Craton indicate that the Nuendah Formation also interfingers with the Gibson Formation (Glassford 1987; Glassford & Semeniuk 1995), although this could not be confirmed at East Yornaning owing to a lack of suitably positioned boreholes or surface exposures.

Correlation. In terms of lithology and stratigraphic position, the Nuendah Formation at East Yornaning correlates with the clayey sand facies of the Nuendah Formation in the north-eastern Yilgarn Craton (Glassford 1987). In the north-eastern Yilgarn Craton, however, this facies of the Nuendah Formation is typically confined to the base of breakaways, whereas at East Yornaning it occurs in most landscape positions. The more widespread distribution of the Nuendah Formation at East Yornaning probably relates to increased fluvial dissection attendant upon a much greater local relief and higher rainfall.

The Quairading Sandstone of Salama (1997) correlates with the Nuendah Formation at East Yornaning in that it too is largely a clayey quartzo-feldspathic sand that infills bedrock-bounded palaeovalleys developed beneath major modern valley floors. The Nuendah Formation is unlikely, however, to correlate with other quartz sandy palaeovalley fills in the region that are overlain by a thick unit of clay (Waterhouse *et al.* 1994; De Silva *et al.* 2000). Palynological evidence suggests that these valley fills are of Eocene age, which is considerably older than the Nuendah Formation (see below) and more similar in age to the Westonia Formation.

Origin. On valley sides the Nuendah Formation has been, and continues to be, principally deposited by unconfined sheet-wash following heavy rains and to all lesser extent by continuous down-slope creep. In valley-side gullies and along the major valley floors the Nuendah Formation is principally deposited within ephemeral fluvial channels and associated flood plains. Palaeovalleys filled with Nuendah Formation beneath the present valley floors may reflect phases of stream rejuvenation arising from tectonic uplift or changes in climate. In view of the catchment's proximity to the western margin of the Great Plateau and Darling Fault, the former seems more likely.

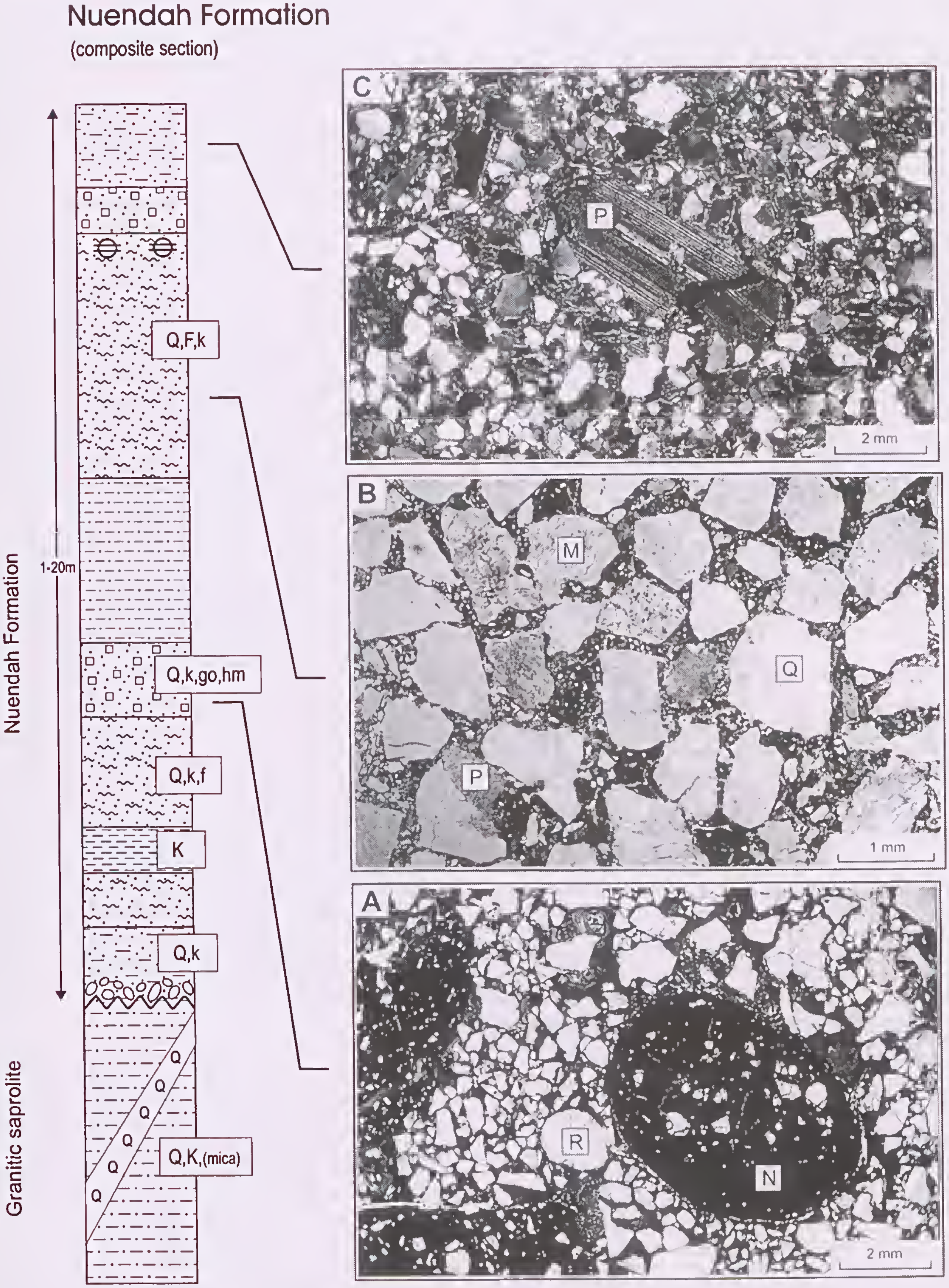

Figure 10. Composite stratigraphic section of Nuendah Formation lithofacies with representative optical photomicrographs. A: Gravelly muddy sand lithofacies. Note rounded quartz grains (R) and ferruginous nodules (N). B: Muddy sand lithofacies. C: Clayey sand. Dominant minerals are quartz (Q), microcline (M), and plagioclase (P). A,B = sample YN43 12.6 m, B = sample EY57/1, C = sample YN43 2.0 m. A cross-polarized light; B,C plane-polarized light.

Provenance. Granitic rock fragments and fresh feldspar within the muddy sand and gravelly muddy sand facies indicate major contributions from fresh granite, with Mulline Formation pisolitic duricrust also contributing significantly to the gravelly muddy sand facies. A decrease in feldspar and granitic rock fragments with depth within the palaeovalleys may simply reflect increased post-depositional weathering with time. Alternatively, it may reflect the progressive stripping of weathered granite (from upper saprolite to saprock) associated with tectonic uplift and incision of the palaeovalleys. The Gibson Formation is also likely to have been an important source for the Nuendah Formation, particularly after Pleistocene arid phases when Gibson Formation sand-sheets would have been more widespread.

Age. The landsurface component of the Nuendah Formation is largely of latest Quaternary (Holocene) age, having been deposited under present conditions of fairly high rainfall and seasonal drainage. The maximum age of the Nuendah Formation is more difficult to establish. However, an early Quaternary age for the base of the Nuendah Formation seems likely on the basis of having interfingering contacts with the Gibson Formation (interpreted as Pleistocene), and that it fills narrow palaeovalleys cut within broader valleys probably formed by epeirogenic uplift of the Great Plateau in the late Tertiary (?Pliocene; Jutson 1934; Bettenay & Mulcahy 1972).

Discussion

Using a non-genetic lithostratigraphic approach, the regolith cover at East Yornaning has been subdivided into six major units, (1) weathered granite (mainly white quartz sandy kaolinitic clay with remnant granitic fabric), (2) weathered dolerite (mainly white slightly quartz sandy kaolinitic clay with remnant interstitial and granophyric fabric), (3) Westonia Formation (mainly light red clayey quartz sand becoming nodular and incipiently pisolitic in uppermost sections), (4) Mulline Formation (mainly red pisolitic sandy aluminous duricrust), (5) Gibson Formation (mainly light grey bimodal quartz sand), and (6) Nuendah Formation (mainly white muddy quartzo-feldspathic sand). Apart from providing a stratigraphic framework for future geological investigations of regolith within the south-western Yilgarn Craton, the results of this study have a number of important implications.

In the absence of clear evidence of transport (cross-stratification, peat beds, basal conglomerate, truncated igneous structures, rounded quartz pebbles *etc*), it may be very difficult to distinguish detrital sediments from weathered crystalline basement. This is because regolith sedimentary strata are typically massive, chemically mature (contain only secondary or ultrastable primary minerals) and texturally immature (have a clay-rich matrix with angular and poorly sorted framework grains), which is very similar to weathered crystalline basement rock. A potential consequence of this similarity is for the sedimentary component of regolith to be underestimated.

The sequence of Gibson Formation sand overlying Mulline Formation pisolitic duricrust overlying Westonia clayey sand, which characterises the interfluve zones at East Yornaning, can readily be mistaken for the sequence of zones produced by the *in situ* chemical weathering of Precambrian granite (Gilkes *et al.* 1973; Sadlier & Gilkes 1976). This error appears to have been made by McArthur *et al.* (1977) in their mapping of the regolith in the East Yornaning and broader Murray River catchments.

Given that the sequence of regolith strata (including pisolitic duricrust) situated along interfluve zones at East Yornaning is largely of sedimentary origin, it seems highly unlikely that a plain underlain by a "laterite" profile formed by the *in situ* weathering of Precambrian basement ("Old Plateau" of Jutson 1934) extended throughout the region, and that the present system of valleys were carved from it. Conceptual models of regolith–landscape development, based on the variable stripping of a regionally contiguous duricrust-capped weathering mantle (Woolnough 1918; Jutson 1934; Mulcahy 1959; Finkl & Churchward 1973; McArthur *et al.* 1977; Mabbutt 1980) are therefore not supported, at least within the East Yornaning area.

As demonstrated by the distribution of the Nuendah Formation, water-laid sediments can be deposited along gently inclined valley side-slopes as well as valley floors. There is therefore no *a priori* need to invoke landscape inversion (*e.g.* Pain & Ollier 1995) to account for ancient fluvial sediments, such as the basal clayey sand facies of the Westonia Formation, that currently occupy upper landscape positions.

The regolith at East Yornaning is polygenetic, containing lithofacies or lithofacies components formed by a variety of processes (*e.g.* alluvial and aeolian deposition, *in situ* chemical weathering, additions and translocation of fines, bleaching of yellow sands by organic acids) that have operated at different times, principally under the influence of climatic and tectonic controls. The sedimentary regolith lithofacies are also largely polycyclic, having been recycled at least in part from pre-existing sedimentary strata. The rounded coarse sand-sized quartz grains at East Yornaning, for example, are likely to have undergone many episodes of erosion, transport, deposition and pedogenesis before being deposited in their present locations.

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Notes on ....

Clutch hydration following oviposition by urination may reduce desiccation in thorny devil (*Moloch horridus*) eggs

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Abstract. During fieldwork in the eastern goldfields, a gravid female thorny devil (*Moloch horridus*) was collected. Whilst held in captivity the female deposited eight eggs in a calico bag and apparently urinated over the clutch. We propose that thorny devils may hydrate their eggs after oviposition to reduce desiccation during development in the nesting burrow. This may lead to a fitness increase for the offspring at hatching in the form of increased hatchling size

Key words: clutch, hydration, *Moloch horridus*, dragon lizard

Introduction

Among oviparous species, optimal nest site selection, nest construction and maintenance of the egg clutch (*e.g.* brooding) can contribute to a reduction in offspring mortality (Covacevich & Limpus 1972; Cooper-Preston 1992; Shine 1998) and increase offspring fitness (Shine 1988).

Desiccation of reptilian egg clutches occurs most rapidly in environments with low water vapour pressure and high thermal conductivity (Ackerman 1994), and in situations where a large proportion of the total surface area of the clutch is exposed to soil or open air (Ackerman & Dmi'el 1985). Consequently, reptiles often deposit their clutch in a burrow that provides thermal stability, higher humidity than ambient or surface conditions, and reduced exposure (Baudinette 1973; Bennett 1988; Roper 2001).

Like other agamids, thorny devils (*Moloch horridus*) lay eggs and excavate their own nesting burrow (Pianka *et al.* 1996; Thompson in press). Eggs are incubated in the burrow for approximately 115 days (range 90-132 days; Sporn 1965; Pianka *et al.* 1996), and during this time there is great potential for egg desiccation. We describe a fortuitous observation of clutch hydration that suggests thorny devils urinate on their egg mass as a mode of parental care to increase offspring fitness. Observations of this nature have previously been described for oviparous reptiles such as skinks (Fitch 1954; Somma & Fawcett 1989), crocodiles (Whitaker & Whitaker 1977) and snakes (Bell & Van den Sande 1986; York & Burghardt 1988; Ross & Marzec 1990; Shine 1998).

Observations

During fieldwork in the eastern goldfields of Western Australia (Koolyanobbing Ranges; 30° 29' S; 119° 30' E) a gravid female thorny devil was collected in open sand plain country. We placed the thorny devil in a calico bag (21 cm x 30 cm) and transferred it to our field station where it was held in a dark enclosure and maintained at temperatures between 18-22 °C. The lizard was monitored daily, and on the fourth day egg deposition had occurred in the calico bag. Eight eggs were deposited in total. In addition, we noticed that the calico bag was saturated with fluid and contained evidence of faeces (ant remnants). We concluded that the female thorny devil had urinated and defaecated over the clutch, resulting in saturation of the eggs and at least half of the calico bag.

Discussion

We suggest that this thorny devil, once confined but left undisturbed, had deposited its clutch and hydrated the eggs as it might do in a nesting burrow in the field. Egg deposition could have been a coincidental observation, or oviposition and defecation could have been a stress induced response to captivity. However, this is unlikely for two reasons. Firstly, reptilian excreta consists mainly of insoluble uric acid and undigested food material and contains very little fluid (Bradshaw 1997). A considerable amount of fluid must have been liberated from the cloaca to saturate the bag to the extent that we observed. Secondly, egg deposition was not likely to be a stress response as the normal response of gravid individuals to stress is egg retention (Hughes *et al.* 1986; Mills *et al.* 1991).

We therefore suggest that urination/defaecation was the action of an individual not unduly stressed by captivity and that clutch hydration in this fashion may be a tactic used by female thorny devils in the field to increase the number of eggs that hatch successfully and increase offspring size (Shine 1988; Shine & Brown in press). Thorny devils burrow in relatively compact substrates, such as red lateritic clays (Thompson in press), and these substrates should be favourable for incubation (*i.e.* humid with stable temperature). However, hydration of the clutch by the adult female during or after oviposition should substantially increase the relative humidity of the burrow and extend the period over which the burrow remains humid. Moreover, most reptilian eggs are permeable to water and potentially hygroscopic, drawing in water if the surrounding medium is sufficiently moist (Seymour *et al.* 1997; Quintana 2001). Urination over the clutch by the adult female may provide water for uptake and increase the total water content of the eggs, and increase offspring size at hatching.

Ackerman & Dmi'el (1985) reported that egg desiccation is accelerated by exposure to open air or dry soil. Thorny devils lay eggs in a chamber, leaving the eggs sitting on (rather than buried in) loose soil (Pianka *et al.* 1996; Thompson in press). Such exposure, even in a burrow, would increase the likelihood of desiccation if burrow humidity were low. Manipulation of an egg clutch by the female after deposition has frequently been reported (see Shine 1988 for summary). Therefore it is not unreasonable to suggest that urination over the clutch may compensate for poor egg position and exposure to air that might otherwise increase egg desiccation.

Such a contribution toward an increase in offspring fitness comes at a cost to the adult. The potential cost paid by the female thorny devil following a contribution to clutch hydration is obviously its survival costs associated with increased water loss. However, these costs are likely to be low, as the thorny devil employs an extremely efficient hygroscopic technique for water acquisition (Bentley and Blumer 1962; Withers 1993), and is probably able to rehydrate relatively quickly after hydrating its clutch, provided water was available.

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THE ROYAL SOCIETY OF WESTERN AUSTRALIA INCORPORATED

Constitution and Rules and Regulations

(Revised March 1996)

Constitution

1. The scientific society known as "The Royal Society of Western Australia Incorporated" (hereinafter referred to as "The Society") has the objects, purposes, and powers hereinafter mentioned.

Objects, purposes, and powers

2. To promote and assist in the advancement of science.
3. To print and publish, or join in printing and publishing, one or more journals, periodicals, books, newsletters or other documents relating to science.
4. To promote, produce and to hold, or join in promoting, producing and holding meetings, lectures, conferences, symposia, excursions and exhibitions in furtherance of any objects of The Society.
5. To found, subsidise or contribute to, for the benefit of any institutions or persons, scholarships, grants, prizes, or monetary or other rewards in connection with all or any of the objects or purposes of The Society.
6. To acquire by purchase, lease, exchange, hire, or by way of loan or otherwise, any real or personal property in furtherance of any objects of The Society.
7. To invest, sell, lease, hire, mortgage, charge, lend, surrender or otherwise dispose of, or deal with all or any part of the assets or property, real or personal, of The Society, or to borrow money and grant security therefore and to liquidate, redeem or discharge any obligations undertaken in furtherance of any objects of The Society.
8. To improve, develop or extend all or any of the property or rights of The Society, also to build, erect or alter any buildings or erections, and to furnish, fit up, and maintain the same and provide fittings, equipment and appliances.
9. To amalgamate, co-operate or affiliate with any other society, association or body having objects wholly or in part similar to those of this Society.
10. To protect or assist in protecting the interests or rights of any member or members of The Society.

Rules and Regulations

Membership

11. The Society shall consist of members who are all individuals involved, assisting or interested in the promotion and/or advancement of science. Members shall be divided into the classes hereinafter mentioned, and the members who are, have been, or may be duly elected as members of such respective classes shall have the rights and privileges hereinafter specified as appertaining to such respective classes, subject always to the due and punctual payment of the annual subscription or other sum hereinafter provided to be paid by the respective members of each class, namely:

    (a) Ordinary Members: An Ordinary Member if financial shall have the following rights and privileges:

    - (i) To be present and to speak and vote at Ordinary, Special or Annual General Meetings of The Society, to vote in postal ballots conducted by The Society, and to attend excursions, meetings, lectures or other activities arranged from time to time by The Society.
    - (ii) To be eligible for election as a member of the Council hereinafter referred to and also to any office or position in The Society.
    - (iii) To submit to the Council for consideration for publication papers prepared on any scientific subject.
    - (iv) To receive the Journal of The Society.
    - (v) To receive other publications or documents issued by The Society, upon such conditions as the Council may from time to time determine.
    - (vi) To borrow books, periodicals, papers, or other documents belonging to The Society, subject to the approval of the Council.
    - (vii) To propose or second candidates for admission as Ordinary, Associate or Student Members of The Society.
    - (viii) At any meeting held by The Society to introduce visitors. Such visitors shall not

be entitled to vote at any such meeting or excursion, but may express opinions on any matter under discussion at the invitation of the chairman or leader.

(ix) To propose or second any Honorary or financial Ordinary Member for election to the Council.

(b) Associate Members: Persons elected as Associate Members shall be entitled to attend and speak at general meetings, excursions and other activities conducted by The Society, but shall not be entitled to vote at any meeting, and if any such member should vote, then that vote shall not be counted. Associate Members shall be entitled to submit papers for publication, but shall not receive the Journal of the Society except at a price fixed by the Council from time to time and subject to the approval of the Council, may borrow books, periodicals or other documents belonging to The Society, but shall not be entitled to be proposed for, or elected to, any office in The Society, nor to propose or second others for membership or office in The Society.

(c) Student Members: The Council may, on application to be made each year in such form it may require, admit as Student Members, persons who are undertaking full-time studies in Western Australia, or as agreed by Council. Student Members shall have the same rights and privileges, and shall be subject to the same restrictions, as Associate Members, except that they shall receive the Journal of the Society.

(d) Honorary Members: The Society at its Annual General Meeting in any year may, on the recommendation of the Council, admit as Honorary Members persons distinguished in Science or as patrons thereof, but only in so far as the number of such members shall not henceforth at any time exceed five percent of the total Ordinary, Associate and Student membership of the Society. Honorary Members shall have the same rights and privileges as Ordinary Members, but without liability for any subscription.

(e) Honorary Associate Members: The Society at its Annual General Meeting in any year may, on the recommendation of the Council, admit as Honorary Associate Members persons interested in science, but only in so far as the number of such members shall not exceed five percent of the total Ordinary, Associate and Student membership of the Society. Honorary Associate Members shall have the same rights and privileges, and be subject to the same restrictions, as Associate Members, but without liability for any subscription.

(f) Corporate Members: Corporate membership may be made available by the Council to organisations under such terms and with such rights and privileges as the Council may determine.

12. Every person desirous of becoming an Ordinary or Associate Member of The Society shall make application in the form prescribed from time to time by the Council and shall be proposed by an Ordinary or Honorary Member of The Society and be seconded by at least two other Ordinary or Honorary Members of The Society, to each of whom the applicant is known personally. Each application shall be accompanied by the subscription applicable to the class of membership sought and shall be lodged with one of the Secretaries. Each Ordinary and Honorary Member of The Society shall be informed of the application forthwith by such means as the Council may from time to time determine. The Council shall accept or reject each candidate at a meeting of the Council held not less than one month and not more than six months after issue of advice of the candidate's application to the Ordinary and Honorary Members. Admission shall be made by a two thirds majority of those Council members present and voting.

13. The Secretary shall inform each candidate of his admission or non-admission to the class of membership sought. Upon admission, Ordinary or Associate Members shall receive a copy of The Society's Constitution and Rules and Regulations. Their membership shall be deemed to apply to the whole of the financial year in which they were admitted so that, subject to their availability, they shall be entitled to receive all publications and documents issued during that year to all members of their class.

14. Members of The Society, of whatever class, shall be bound to observe and perform, and not commit any breach of, the Rules and Regulations of The Society from time to time in force.

15. Members shall notify the Secretary in writing of their address for receiving notices or communications to be forwarded to them, and shall from time to time notify in writing any change in such address. If any member shall fail to give such notification they shall have no claim against The Society for publications or notices of the meetings or other activities of The Society; notification is deemed to have occurred at the time of posting.

16. Members, on paying to The Society all subscriptions or moneys owed by them and returning all books, papers, manuscripts, or property of The Society which they may have borrowed or received, may resign their membership by giving notice in writing to the Secretary of The Society; and any members ceasing by resignation, death, or otherwise to be a member of The Society shall not, nor shall their representatives have any claim upon or interest in the funds or property of The Society; but nothing herein contained shall prejudice the right of The Society to recover any moneys owing or property of The Society borrowed, held, or received by members at any time.

17. Members whose subscription may be in arrears for a period of more than two years shall, on a resolution of the Council being at any time thereafter passed, be declared to be no longer members and thereupon shall cease to have the rights and privileges to which they may have been entitled, provided always that

nothing herein contained shall prejudice the right of The Society to recover from such members all moneys or subscriptions due, owing, or payable by them up to the date of such termination of their membership, and also to recover all books, papers, manuscripts or property belonging to The Society which may be held or have been received by such members at any time.

18. Members in the respective classes of membership in The Society shall use their best efforts to promote the objects of The Society and shall not do or commit any act, deed, or thing which may be deemed by the Council to be prejudicial to the interests of The Society.

19. The Council may, by an affirmative vote of two thirds of its total membership, remove or suspend from membership or expel any member of The Society. Notice of such removal, suspension, or expulsion, shall be sent by registered post to the last known address of the member concerned within seven days after the decision of the Council. Members against whom such decision of removal, suspension, or expulsion shall be made, shall be entitled to appeal to a Special General Meeting of The Society by notice to be forwarded by them in writing, addressed to the Secretary within two months after the date of such removal, suspension, or expulsion, stating in such notice the grounds of appeal. It shall be the duty of the Council to summon a Special General Meeting of The Society for the purpose of considering any such appeal, and of hearing statements by any Member of the Council or by the member who may have been removed, suspended or expelled, and if a majority of the members present at such meeting uphold the decision of the Council, then the decision of the Council shall be confirmed, but if such majority shall uphold the appeal, then the decision to remove, suspend, or expel such member shall be set aside. No members shall be entitled to exercise such right of appeal after the expiration of the said period of two months. In the event of any such removal, suspension, or expulsion taking effect, any members concerned shall remain liable for all moneys or subscriptions due or payable by them as at the date of such removal, suspension, or expulsion, and for the return of all property belonging to The Society.

Subscriptions

20. The subscription for each ordinary membership shall be set from time to time on recommendation of the Council and approval by a resolution passed by a two-thirds majority of Ordinary Members voting at any Ordinary or Annual General Meeting of The Society, of which at least twenty eight days notice has been given, and in which notice the proposed alterations have been specified.

    Ordinary Members whose subscriptions are not in arrears shall be granted Ordinary Membership for Life upon payment of a fee of twenty years subscription at the rate of the current year.

21. Associate Membership shall not be more than 60 percent of the Ordinary Membership rate.

22. Student Membership shall not be more than 60 percent of the Ordinary Membership rate.

23. The financial year of The Society shall be from the first day of July in each year to the thirtieth day of June in the following year.

24. All subscriptions shall be payable in advance and shall become due on the first day of July in each year. Any member whose subscription is unpaid six months after the due date in any year shall be deemed to be not financial. After this date a late fee shall be payable at a rate determined by Council from time to time.

Management

25. The management of the business and affairs of The Society shall be vested in a Council consisting of a President, two Vice-Presidents, Treasurer, three Secretaries, Librarian, Editor, Journal Manager, Immediate Past President and seven Ordinary or Honorary Members of The Society.

26. All members of the Council shall be elected at the Annual General Meeting of The Society to be held on a date normally in July at a place to be decided by the Council and serve for a term of one or two years. For the purpose of such election the Council then in office shall submit, at an Ordinary or Special General Meeting held not less than one calendar month before the Annual General Meeting, a list of names of Honorary or financial Ordinary Members proposed by the Council for election indicating the length of term of office and shall appoint a Returning Officer. Any Ordinary or Honorary Member present at such Ordinary General Meeting shall be entitled to propose another financial Ordinary or any Honorary Member to hold any position on the Council, and if such nomination be duly seconded and if the candidate nominated has signified willingness to accept office if elected, then the name of such nominee shall be added as a candidate. Further, any Ordinary or Honorary Member of The Society may lodge with the Returning Officer within seven days after that Ordinary or Special General Meeting, preceding the Annual General Meeting, a nomination in writing in favour of any financial Ordinary or any Honorary Member for any position on the Council. Such written nomination shall be seconded by another Ordinary or Honorary Member, and shall carry a statement by the candidate nominated as to their willingness to accept the office if elected. Upon receipt of such nomination, the Returning Officer shall add the name of the nominee as a candidate for the Council.

27. If the number of members duly proposed for election does not exceed the number of vacancies for the various offices, the Chairman of the Annual General Meeting shall declare the persons nominated as duly elected. If the number of nominations for any office exceeds the number of vacancies, an election shall be held and the results ascertained by preferential ballot. For the purpose of such election, a ballot paper containing the names of all persons duly proposed for all contested positions

on the Council shall be prepared by the Returning Officer and sent to all Ordinary and Honorary Members. Such members desirous of voting shall cause to be delivered to the Returning Officer such ballot papers, duly completed in accordance with any instructions on voting procedure before the formal opening of the Annual General Meeting. The Annual General Meeting shall appoint at least two scrutineers, who shall examine the procedures of the Returning Officer in the counting of votes and who shall report the results of the count to the Chairman of the Annual General Meeting. Such Chairman shall announce the result of the ballot at the Annual General Meeting or at the next Ordinary or Special General Meeting of The Society.

28. All members of the Council shall be eligible for re-election.

29. Any casual vacancy in the Council may be filled by resolution of the Council, and any member so appointed shall hold office until the next annual election of Council. Any vacancy not filled at the annual election shall be deemed a casual vacancy.

30. The Council may define the duties of the three Secretaries and may add any distinguishing word to the title of any or all Secretaries in accordance with the nature of the duties to be performed.

31. The Council shall meet at least once in each month from February to November inclusive in each year (unless otherwise decided by Council), at such times and places as may be appointed by the President, or in the President's absence, by one of the Vice-Presidents, and due and sufficient notice shall be previously sent to each member of the Council.

32. A quorum for a meeting of the Council shall be the President or one of the Vice-Presidents, a Secretary who may be specially appointed for that meeting, and four other members of the Council, and no business shall be transacted at any Council meeting unless such quorum is present.

33. If any members of the Council (including holders of offices) shall fail to attend three consecutive meetings of the Council without satisfactory explanation or reason, or without leave of absence having been first granted to them, then the position or office of such member may by resolution of the Council be declared vacant, and on passing of such resolution they shall cease to be a member of Council and holder of any office to which they may have been elected.

34. Council shall inform members of activities of the Society including deliberations of the Council by publishing and distributing to the members a Proceedings following each Ordinary or Annual General Meeting.

35. The Council shall present at each Annual General Meeting a report giving a review of the work of The Society during the preceding year and some details and information with regard to its progress and affairs, and shall publish this report.

36. The Council may appoint a Committee from among the financial members of the Society, and by two thirds majority resolution may include non-members in such a Committee. A Committee may be of such number as the Council may decide and may consider and make recommendations on any subject on which Council may require advice, provided that such a Committee includes at least one Council Member. Each Committee so appointed shall be reviewed at regular intervals to be determined by the Council.

37. The Council may from time to time make, alter, and repeal by-laws to enable it more effectually to carry out the management of the affairs of The Society, and to regulate the conduct of members and assist in the protection of its property, and for such purposes as may be calculated to advance the welfare of the Society, provided that such changes are not inconsistent with these Rules and Regulations.

38. The Council, without limiting its general powers of management and carrying on the business and affairs of The Society, may exercise and do all things necessary except such as may be required or directed to be exercised by General Meetings, including power to appoint and remove all or any officers, assistants, employees, or others deemed by the Council to be necessary in connection with the work of The Society, and that with or without remuneration and upon such terms and conditions as the Council may think fit. The Council may also delegate all or any of its powers or authorities to any committee or sub-committee from time to time, and may pay all or any expenses or liabilities incurred from time to time and take any steps or proceedings which may be deemed desirable for the purpose of carrying out or securing the fulfilment of any of the objects or purposes of The Society.

President and Vice-Presidents

39. The duties of the President shall be to preside at all meetings of The Society and Council, and regulate all the proceedings therein and generally to execute or see to the execution of the Rules and Regulations and by-laws of The Society. In the case of an equality of votes at any meeting, the President or Vice-President or member presiding shall have a casting vote in addition to a deliberative vote.

40. In the absence of the President from any meeting of the Council, the President's place shall be filled by one of the Vice-Presidents. In the absence of the President from any other meeting or excursion of The Society, the President's place shall be filled by one of the Vice-Presidents or by an Ordinary or Honorary Member of The Society elected as Chairman or leader by the Ordinary and Honorary Members there present.

Duties of Officers

41. The Secretaries shall conduct correspondence, arrange meetings, cause notices of meetings and Proceedings to be sent out, keep adequate records of all meetings, membership and other activities of The Society, and generally perform such duties as are

usually assigned to persons holding such office and comply with the directions, requests, or instructions issued from time to time by the Council.

42. The Treasurer shall keep a correct record of all receipts and disbursements, including subscriptions and all moneys received for the benefit of The Society, and shall pay those moneys forthwith to the credit of The Society at its bankers. It shall be the duty of the Treasurer to pay all accounts passed by the Council. No moneys shall be withdrawn from the bank account except by cheque signed by any two of a group of three or more members of the Council which shall include the Treasurer and two or more other members of Council so authorized by Council. The Treasurer shall cause the books of The Society to be posted regularly, and shall bring his books to balance as on the thirtieth day of June in each year, or on such other date as the Council may from time to time decide.

43. The Treasurer shall annually submit to an Auditor or Auditors all books and accounts kept by the Treasurer in connection with the affairs of The Society, made up to the date last mentioned. The Society shall, not later than its Ordinary General Meeting immediately prior to the Annual General Meeting, appoint an Auditor or Auditors, but if such Ordinary General Meeting shall fail to make such appointment, then the Council may appoint an Auditor or Auditors.

44. It shall be the duty of the Auditor or Auditors of The Society to submit a written report each year on the financial affairs of The Society through the Council to an Ordinary, Special or Annual General Meeting of The Society.

45. The Librarian shall maintain records and generally manage the books, periodicals and documents of The Society according to the directions of the Council.

46. The Editor shall supervise the production of The Society's Journal and such other publications as the Council may direct.

47. The Journal Manager shall supervise the distribution of The Society's Journal and other publications as authorized by Council.

48. Other members of the Council shall assist in the general management of The Society according to the needs which may arise from time to time.

Ordinary General Meetings

49. Ordinary General Meetings of The Society shall be held at 8 p.m. on the third Monday of the months March to June and August to December inclusive in each year, unless the Council determines otherwise, but at least three Ordinary General Meetings shall be held in each financial year. Notice of each Ordinary General Meeting shall be sent to all members of each class. A quorum for an Ordinary General Meeting shall be seven Ordinary or Honorary Members personally present. Conduct of an Ordinary General Meeting shall be at the discretion of the President or Chairman elected by such meeting.

Annual General Meetings

50. The Annual General Meeting of The Society shall, unless the Council determines otherwise, be held on the third Monday of July in each year at a time and place determined by the Council. Notice of each Annual General Meeting shall be sent to all members of each class at least one calendar month before such meeting.

51. The proceedings of the Annual General Meeting, unless otherwise determined by the Council, shall be as follows:

    (a) Presentation of the minutes of the previous Annual General Meeting.

    (b) Reading of nominations of candidates for Council, and, if necessary, appointment of scrutineers, and counting of votes.

    (c) Presentation of the Annual Report of the Council.

    (d) Presentation of the Balance Sheet, Statement of Accounts and (if available) Auditor's Report.

    (e) Report (if necessary) of the scrutineers on the ballot and declaration of the results by the retiring President.

    (f) Address by the retiring President.

    (g) Installation of the new President.

    (h) Any other business of which notice may have been given prior to or agreed during the meeting to be considered.

52. A quorum for transaction of business at an Annual General Meeting shall be seven Ordinary or Honorary Members of The Society personally present.

Special General Meetings

53. Special General Meetings of The Society may be called by the Council whenever it may deem such meeting expedient, or on the requisition of ten Ordinary or Honorary Members made in writing to one of the Secretaries and specifying the purpose for which the meeting is required. Upon receipt of such requisition, that Secretary shall call the meeting within not less than seven days nor more than twenty eight days. Notice of such meeting shall be sent to all members of each class. The meeting shall be chaired by the President or a Vice-President or, in their absence, an Ordinary or Honorary Member elected by the meeting.

54. A quorum for a Special General Meeting of The Society shall be seven Ordinary or Honorary Members personally present.

The Journal of the Society

55. The Society shall publish a Journal at least once a year, in which papers communicated to The Society during or before that year may be printed. The Journal shall be printed in such form as decided by the Council.

56. Every paper intended to be published in the Society's Journal must be sent to the Editor for

consideration by Council. The Editor shall Chair a Publications Committee, if such is appointed by Council, to provide assistance and advice to the Editor.

57. The Editor shall seek an expert opinion from any person or persons the Editor may select as referees to judge the suitability of any paper for publication. The Editor shall recommend to the Council whether or not a paper submitted for publication should be accepted for the Society's Journal. A paper of which the Editor is author or co-author shall be edited by a member of Council, so authorised by Council, who is not a co-author of the paper.

58. It shall be the duty of the Council to decide, on the recommendation of theEditor or authorised Council member, whether or not a contribution shall be accepted for publication.

59. Publication in the Society's Journal shall be available to all categories of members.

60. The original copy of every paper accepted for publication by The Society, with its illustrations, shall become the property of The Society, unless the Council decides otherwise. Authors shall not be at liberty to publish elsewhere papers submitted to The Society for publication in its Journal, unless permission for doing so is given by the Council, or unless the Society fails to publish the paper in the Journal of the year in which it is accepted or of the succeeding year, or does not accept the paper for publication.

61. The published price of the Journal shall be fixed by the Council from time to time.

62. Offprints of papers shall be available to authors on such terms as shall be decided from time to time by the Council.

The Medal of the Royal Society of Western Australia

63. A Medal, for which Council will call for nominations through its Proceedings, shall be awarded by the Council every fourth year or at such other times or periods as the Council may from time to time decide for distinguished work in science connected with Western Australia. The Council shall appoint a Medal Committee consisting of five members of the Council to assess the nominations and recommend a recipient of the Medal. The recipient shall, on the awarding of the Medal, be requested to deliver a public address to be known as the Royal Society of Western Australia Medal Lecture.

Formation of Sections

64. Sections may be formed for the purpose of any particular branch of science. Any member of The Society may be enrolled as a member of one or more sections. Each section shall appoint a Chairman and Secretary, with the approval of Council. Sections shall not incur expenditure without first obtaining the approval of the Council. Any communication to a section may be presented subsequently at a general meeting of The Society.

Common Seal

65. The Common Seal of The Society shall be in the custody of the President or one of the Vice-Presidents, and the President or any one Vice-President shall respectively be authorized to use the same, and when required to be affixed to any deed, document, or writing, shall be so affixed and signed by either the President or one of the Vice-Presidents and countersigned by a Secretary of The Society.

Interpretation of the Constitution and Rules and Regulations

66. The Council of The Society shall be the sole authority for the interpretation of the Constitution and of the Rules and Regulations of The Society, and the decisions of the Council on questions of interpretation shall be final and binding on all members.

Alteration of the Constitution and Rules and Regulations

67. The Constitution or the Rules and Regulations or any of them may be amended, altered, enlarged or repealed from time to time by a resolution passed by 75 percent of Ordinary or Honorary Members voting in a postal ballot conducted by the Council. Notice of intention to conduct such a ballot shall be given with notice of an impending Ordinary or Annual or Special General Meeting of The Society and the proposed amendment or amendments shall be presented at that meeting at least one calendar month before the ballot is held.

Non-Profit Organisation

68. The Society is operated as a non-profit organisation. The assets and income of The Society shall be applied solely in furtherance of its above mentioned objects and purposes and no portion shall be distributed directly or indirectly to the members of The Society except as bone fide compensation for services rendered or expenses incurred on behalf of The Society.

Winding up of The Society

69. The Society may be wound up by a resolution to be passed by a four fifths majority of the Ordinary and Honorary Members of The Society present and voting at a Special General Meeting summoned for such purpose, whereof at least twenty eight days notice shall be given. If a resolution to wind up The Society be passed, and there remains, after satisfaction of all The Society's debts and liabilities including the costs, charges and expenses of that winding up, any property whatsoever, the same shall not be paid to or distributed among the members but shall be given or transferred to some other association or associations which are themselves incorporated under the Associations Incorporation Act 1987 and are therefore non-profit organisations, or for charitable purposes, or both, as determined by resolution of the members.

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Call repertoire of an Australian treefrog, *Litoria adelaidensis* (Anura, Hylidae)

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Abstract

Litoria adelaidensis (Anura: Hylidae) has a call repertoire that includes two structurally different call types. Males produced three recognizable pulsed calls (call types 1 to 3) and one unpulsed call (call type 4). All call types have two distinct frequency peaks. Call type 1 was produced most often, suggesting that this signal functions to attract females. Call type 4 was rarely produced and may be associated with male-male interactions, as males in close proximity to each other were observed making this call. The purposes of call types 2 and 3 are unknown. The different calls may be part of a graded response incorporating both male-male interaction and female attraction.

Key words: frog, vocal repertoire, advertisement call, acoustic communication, Hylidae, *Litoria adelaidensis*

Introduction

Organisms that emit acoustic signals often have a repertoire of calls, the extent of which reflects the strength and complexity of both sexual and natural selection (Narins *et al.* 2000). Female frogs typically use the male call to locate and choose between potential mates and may therefore impose strong selection on call structure (Gerhardt 1994). Male frogs can use acoustic signals in response to physical and/or acoustic intrusions by other males (Narins *et al.* 2000) and may use conspecific calls to determine the proximity (Brenowitz *et al.* 1984), size (Davies & Halliday 1978; Wagner 1992) and possibly condition of rivals (Halliday & Tejedo, 1995). Although many species use a single call for both functions (*e.g.* Littlejohn 1977; Wells 1977; Halliday & Tejedo 1995), a number have developed more complex signal repertoires (*e.g.* Given 1987; Narins *et al.* 2000) in which different calls serve different functions (*e.g.* Robertson 1984; Littlejohn & Harrison 1985).

Male frogs can produce acoustic signals that differ in both temporal and spectral structure (*e.g.* Ovaska & Calbeck 1997; Jehle & Arak 1998). *Hyla regilla* provides an excellent example, as it produces three distinct signals with similar spectral characteristics but different temporal properties (Brenowitz *et al.* 2001). A diphasic "advertisement call" is emitted commonly throughout the night and appears to attract females and to influence male spacing (Whitney & Krebs 1975a,b). A monophasic "advertisement call" is emitted at a high rate when females approach and is produced until the male has entered into amplexus with the female, but its exact function remains unclear (Brenowitz *et al.* 2001). *Hyla regilla* also produce an "encounter call" that is believed to be an aggressive signal that is important in the establishment of spacing between calling males (Brenowitz *et al.* 2001). Males will switch to the encounter call after hearing the signal of an "intruding male".

Not only do male frogs often produce several different signals, but the signals may vary in a graded fashion from one extreme to another or from one call to another (Gerhardt & Huber 2002). Graded signals are typically produced in response to external stimuli such as conspecific male calls and/or physical intrusions or the approach of a potential mate. The advertisement call of *Rana nicobariensis*, for example, varies considerably in duration (approximately 20 fold) and the duration of the call is inversely related to the distance between the focal calling male and his nearest calling neighbour (Jehle & Arak 1998). Further, some species produce compound calls that incorporate both advertisement and aggressive signals (*cf* Jehle & Arak 1998). Accordingly, the degree of within and between species variation in the acoustic signals of frogs contrasts with the view of early researchers that the calls of anurans were highly stereotyped and discrete (*e.g.* Blair 1958; Bogert 1960). The acoustic signals made by frogs show great variability which can be generated by natural, inter-sexual and intra-sexual selection (Gerhardt & Huber 2002).

A first step in studying anuran vocalizations is to record and quantify the types of calls that are produced by a species and to associate them with possible functions. Although there are extensive data on calls of Australian myobatrachid frogs (*e.g.* Littlejohn 1959; Littlejohn & Main 1959; Roberts & Wardell-Johnson 1995; Roberts 1997) and investigations of their function (*e.g.* Robertson 1984; Littlejohn & Harrison 1985; Gerhardt *et al.* 2000), comparatively few studies have investigated the call structure or call function for Australian hylid species. Here we quantify the acoustic signals of a south-western Australian frog, the slender treefrog, *Litoria adelaidensis*. The vocal repertoire of this species has not been described, but anecdotal evidence suggests that *L. adelaidensis* emits several different calls.

Materials and methods

Terminology

Anurans typically produce an advertisement call that is used to attract females and in some species to also mediate male-male interactions (Littlejohn 1977). In addition to the advertisement call, repertoires often include separate signals that function in male-male interactions such as an aggressive call, encounter call, or rivalry call (hereafter referred to as aggressive calls; Gerhardt & Huber 2002). Frogs may also produce short-range courtship signals (Gerhardt & Huber 2002) and/or distress and release calls (Bogert 1960). The advertisement call is usually repeated quasi-periodically for many hours per night during the breeding period (Narins *et al.* 2000). The aggressive calls are typically emitted in response to physical encounters with other males and/or when the calls of conspecific males exceed some threshold intensity (Brenowitz *et al.* 2001). Aggressive calls may also be emitted in response to physical or acoustic interactions with heterospecifics (Gerhardt 1994).

Males of a number of species have developed considerable plasticity in their acoustic responses (*cf* Brenowitz *et al.* 2001). Nonetheless, the different signals produced by a male are typically spectrally and/or temporally distinct (Narins *et al.* 2000) and accordingly can be recorded, measured and categorised. We visually examined recording sequences and used conventional statistical analyses to look for consistently distinct acoustic signals with respect to spectral and/or temporal structure.

Recording methods

Calls of fourteen frogs in total were tape-recorded on the 21 August 2000 and 21 September 2000 at Perry Lakes, Perth, Western Australia (31° 56' 40" S, 115° 46' 50" E). Calling males were concentrated along approximately 40 m of shoreline, and the chorus contained about 40 calling males on both occasions. Frogs called from emergent macrophytes and were usually perched between 5 and 60 cm above the water level.

Recordings were made on a Sony Professional Walkman (WM-D6C; frequency response for type I cassette 40 - 15,000 Hz; ± 0.3% tape speed variation; manufacturers specifications) with a Beyer Dynamic M88N (C) microphone. Snout-vent length (± 1 mm) was obtained for 11 of the 14 frogs by placing the dorsal surface of the frog flat against a plastic ruler. Dry-bulb air temperature at each call-site (± 0.2 °C) was measured using a Miller & Weber cloacal thermometer directly after the calling sequence of each frog was recorded. Temperatures ranged from 11 to 16 °C (14.7 ± sd 1.9 °C). Frogs were recorded for a minimum of 3.5 minutes (mean 5.2 ± sd 0.45). Calls were sampled at 44.1 kHz and analyzed using Cool Edit Pro (Syntrillium Software Corporation, Phoenix, v 1.2) running on an IBM microcomputer.

Seven call properties were measured following the procedures of Littlejohn *et al.* (1993) and Gerhardt & Huber (2002). The call properties measured were call duration (ms), pulse number, pulse duration (ms), pulse rate (pulses s^{-1}), low frequency peak (kHz), dominant frequency peak (kHz), and inter-note duration (ms). Pulse rate for call type 2 (see results) is reported as the average of the two notes. Dominant and low-peak frequencies (Fig 1) were measured from a power spectrum of the entire call. Where a significant relationship was detected, call properties were standardized for temperature by converting them to the average call site temperature for the recordings used in this study (14.7 °C). To allow the determination of the direction of relationships, slopes (b_y) are reported with all regression analyses. The first ten males to produce between three and five of each call type were used to investigate the differences between call types. Variation in each call property between call types 1, 2 and 3 were analysed with single-factor ANOVA (Diekhoff 1992). We also performed a discriminant function analysis (DFA; Diekhoff 1992) with the call properties as the dependent variables and three call types as the independent variable. All statistical analyses were conducted with Statistica (v 5.0).

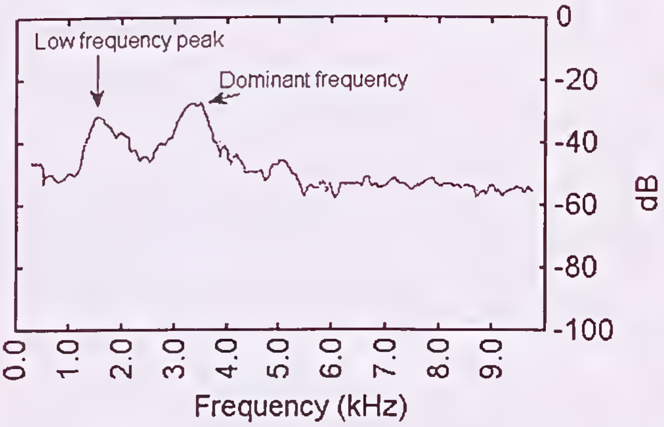

Figure 1. Power spectrum derived from a type 1 call shows the two peaks used to obtain the low frequency peak and dominant frequency.

Results

Call types

The number of calls recorded for each frog varied from 4 to 109 (mean 37.5 ± 6.9). The waveforms revealed four distinct calls (Fig 2). Call type 1 was a pulsed call.

Table 1

Descriptive statistics for properties of call types 1, 2 and 3 of *Litoria adelaidensis*. Values are mean ± sd; sample size is 10 for each call property.

	Call type 1	Call type 2	Call type 3
Call duration (ms)	105.6 ± 26.5	165.2 ± 51.0	46.2 ± 11.5
Pulse number	9.8 ± 1.6	6.7 ± 1.8	2.7 ± 0.41
Pulse duration (ms)	8.1 ± 0.96	9.7 ± 1.5	10.3 ± 3.1
Pulse rate (pulses s^{-1})	86.5 ± 12.0	66.5 ± 15.3	41.2 ± 5.7
Low peak frequency (kHz)	1.8 ± 0.05	1.8 ± 0.06	1.8 ± 0.03
Dominant frequency (kHz)	3.8 ± 0.14	3.8 ± 0.16	3.7 ± 0.12
Inter-note duration (ms)		78.2 ± 33.9	

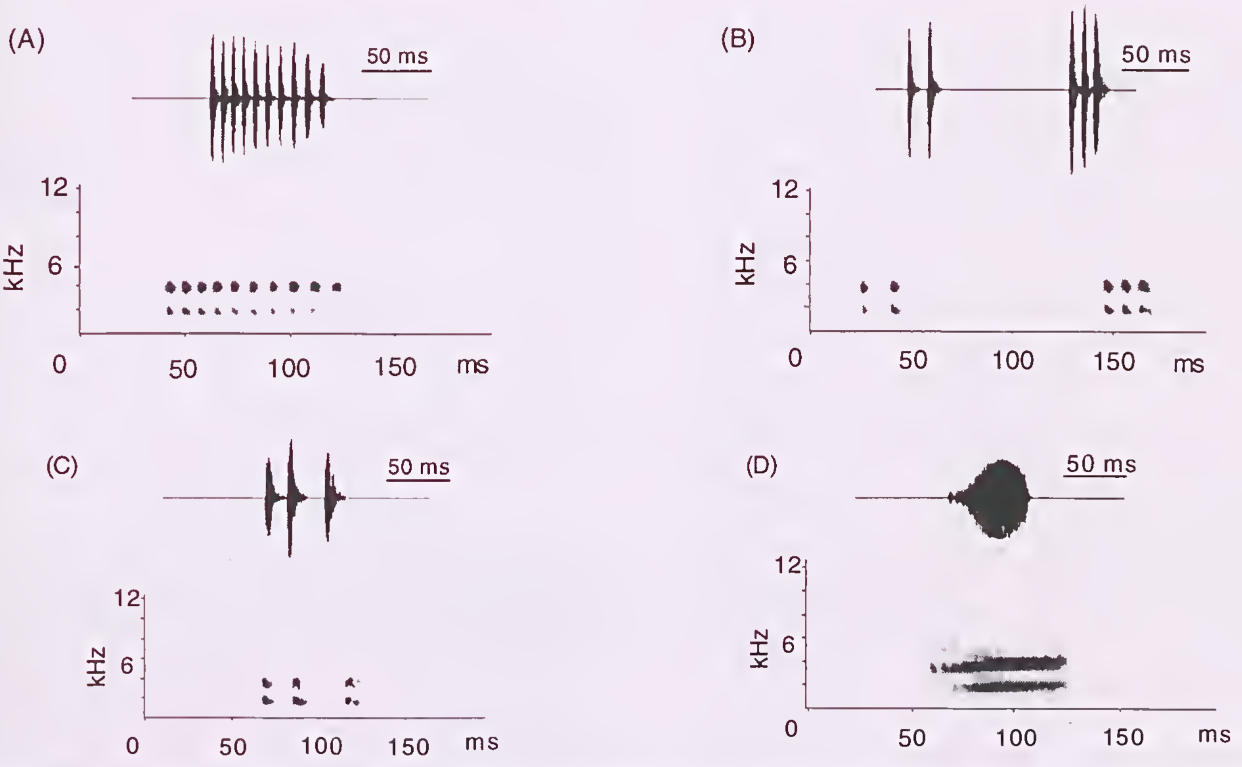

Figure 2. Waveforms (upper) and audiospectrograms (lower) of four types of acoustic signals produced by males of *Litoria adelaidensis*. (A) call type 1, (B) call type 2, (C) call type 3 and (D) call type 4.

Call type 2 was similar to call type 1, but had two pulsed notes with a mean inter-note duration of 78.2 ms (maximum = 136.0 ms). All other calls consisted of a single note only. Call type 3 was a short pulsed call that was similar in duration to one of the notes in call type 2 (Fig 3). Call type 3 was consistently shorter in duration and had fewer pulses (Fig 3) than the other call types. Call type 4 was only recorded from one individual but was often heard in choruses; it was an unpulsed whistle (n = 3, call duration 65.3 ms, low frequency peak 1.7 kHz, dominant frequency peak 3.5 kHz). All pulsed call types had two distinct frequency peaks (Figs 1 and 2) with the higher, or dominant, frequency peak the louder of the two (Table 1).

Variation with temperature

A significant amount of the variation in the both frequency peaks in call types 1, 2, and 3 was explained by differences in temperature. For low peak frequencies; call type 1: $r^2 = 0.66$ and $b_y = 0.04$ ($F_{1,8} = 15.6$, $P < 0.01$); call type 2: $r^2 = 0.62$ and $b_y = 0.04$ ($F_{1,8} = 13.1$, $P < 0.01$); and call type 3: $r^2 = 0.85$ and $b_y = 0.04$ ($F_{1,8} = 43.6$, $P < 0.01$). For dominant peak frequencies; call type 1: $r^2 = 0.60$ and $b_y = 0.09$ ($F_{1,8} = 11.9$, $P < 0.01$); call type 2: $r^2 = 0.6$ and $b_y = 0.10$ ($F_{1,8} = 13.9$, $P < 0.01$); and call type 3: $r^2 = 0.77$ and $b_y = 0.10$ ($F_{1,8} = 26.7$, $P < 0.01$).

Variation with body size

A significant amount of variation in dominant frequency was explained by body size for call types 1, 2 and 3. For call type 1: $r^2 = 0.61$ and $b_y = -0.02$ ($F_{1,8} = 12.6$, $P < 0.01$); call type 2: $r^2 = 0.53$ and $b_y = -0.03$ ($F_{1,8} = 9.1$, $P < 0.05$); call type 3: $r^2 = 0.40$ and $b_y = -0.02$ ($F_{1,8} = 5.4$, $P < 0.05$). The low-frequency peak did not vary significantly with body size for any of the call types (call type 1: $F_{1,8} = 0.80$, $P = 0.40$, call type 2: $F_{1,8} = 1.3$, $P = 0.28$, call type 3: $F_{1,8} = 4.2$, $P = 0.07$).

A significant amount of the variation was explained by variation in body size for call duration and pulse number in call type 1 ($r^2 = 0.46$, $b_y = -6.8$, $F_{1,8} = 6.9$, $P < 0.05$ and $r^2 = 0.57$, $b_y = -0.65$, $F_{1,8} = 10.7$, $P < 0.05$, respectively) and call duration and inter-note duration in call type 2 ($r^2 = 0.55$; $b_y = -16.2$, $F_{1,8} = 9.7$, $P < 0.05$ and $r^2 = 0.47$, $b_y = -9.5$, $F_{1,8} = 7.1$; $P < 0.05$, respectively).

Among call type analyses

The three pulsed-calls varied significantly from each other in call duration ($F_{2,36} = 37.3$, $P < 0.01$), pulse number ($F_{2,36} = 57.8$, $P < 0.01$) and pulse rate ($F_{2,36} = 22.4$, $P < 0.01$, Fig. 3) only. Call type 2 could be differentiated by the presence of two notes. Call types 1 and 3 could be differentiated by their pulse number and duration (Fig 3).

Call type 1 was produced most commonly (mean of the percentage of calls that were call type 1 for each individual = 60.3 ± 6.6%) followed by call type 3 (24.0 ± 5.7%) and call type 2 (15.3 ± 3.7%). The individual that produced the type 4 calls did so on three occasions.

Discriminant analysis

The results of DFA confirmed the univariate analyses, showing that call types 1, 2, and 3 differed from each other in call duration, pulse number and pulse rate (Wilk's $\lambda = 0.02$, approx $F_{12,44} = 25.1$, $P < 0.01$; Fig 4). Even though some overlap occurred between call types in call duration, pulse number and pulse rate (Fig 3), the DFA produced clear separation of each call type (Fig 4).

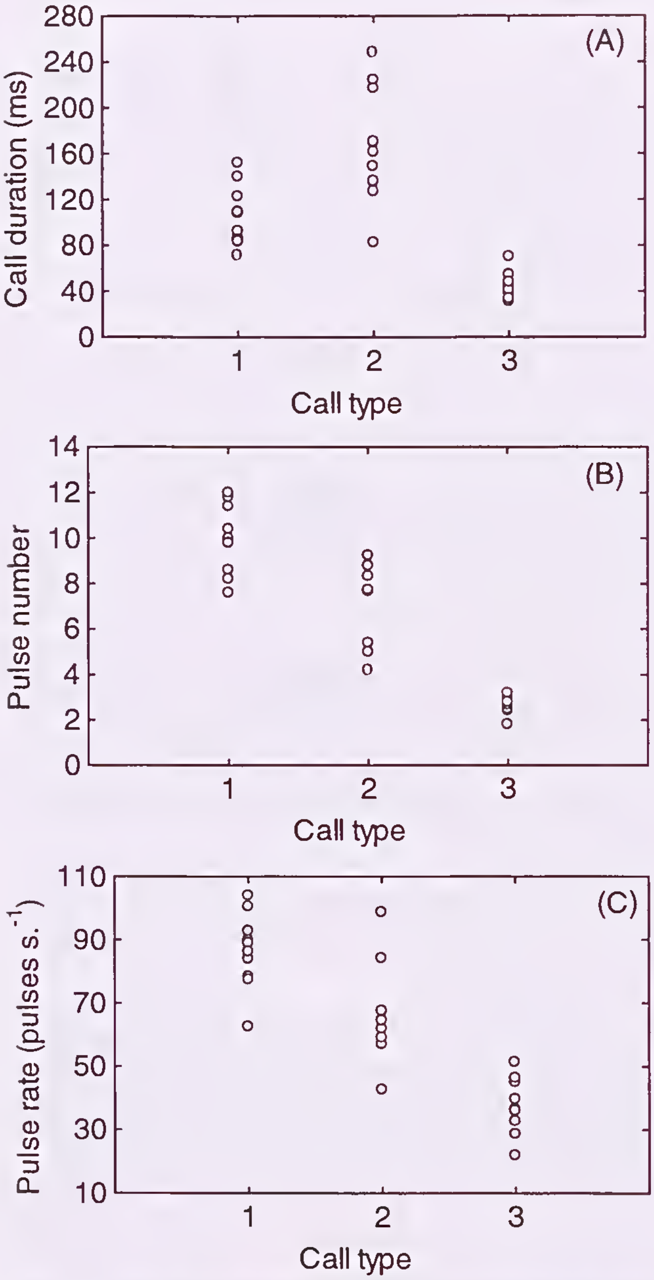

Figure 3. Scatter plots showing differences between the three call types of *Litoria adelaidensis* in (A) call duration, (B) pulse number and (C) pulse rate.

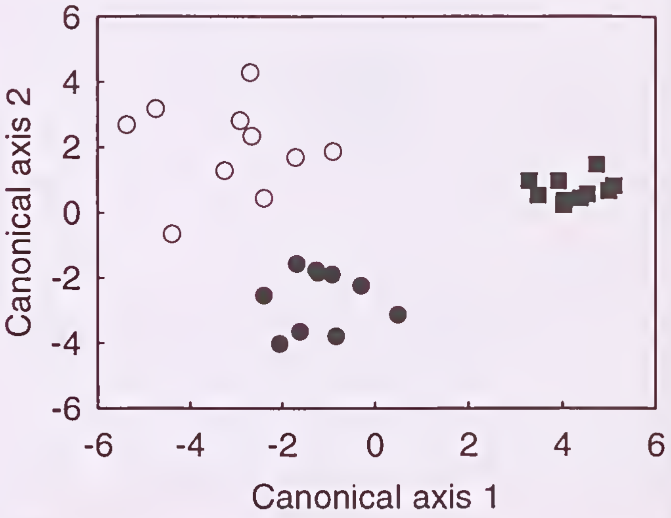

Figure 4. Distribution of the call types (1: solid circle, 2: open circle, and 3: solid square) of male *Litoria adelaidensis* along two canonical discriminant axes derived from a DFA of call properties on call type. The correlations between canonical axis 1 and call duration, pulse number, pulse rate, pulse duration, low frequency peak and dominant frequency were -0.45, -0.50, -0.39, 0.06, -0.10, and -0.11 respectively. The correlations between canonical axis 2 and call duration, pulse number, pulse rate, pulse duration, low frequency peak and dominant frequency were 0.20, -0.67, and -0.53, 0.20, 0.13, and -0.01 respectively.

Discussion

The slender treefrog *Litoria adelaidensis* has a repertoire of acoustic signals that includes both pulsed and unpulsed calls. Four call types were recognised; call types 1, 2 and 3 were pulsed and call type 4 was unpulsed. All call types had two main frequency peaks. The presence of two frequency peaks has been shown to be an important factor in female mate choice in other hylid species (*e.g. Hyla versicolor*; Gerhardt & Huber 2002) and consequently may influence female mate choice in *L. adelaidensis*. This awaits further study.

Only dominant frequency varied consistently with male size across all pulsed call types. A negative correlation between dominant frequency and body length is usual in frogs (Gerhardt 1994) and is probably related to the size of the male's vocal chords (McAlister 1961). The durations of call types 1 and 2 also varied inversely and significantly with body size, as larger males produced shorter calls. Accordingly, the relationships between body size and both frequency and call duration suggest that size and possibly age (frogs generally increase in size with age) may influence male calling tactics in this species. However, the relationship between size and frequency does not hold for all species (*e.g.* Lardner & bin Lakim 2002)

The pulsed calls (call types 1, 2 and 3) differed in temporal structure (in particular, the number of pulses and presence or absence of more than one note). Similar variation in temporal structure of different calls in the repertoire of several species has been reported (*e.g.* Jehle & Arak 1998; Narins *et al.* 2000; Brenowitz *et al.* 2001). The occurrence of significant variation in the temporal but not spectral structure of the calls of *L. adelaidensis* may indicate different selection regimes and/or differential responses to selection. For example, there may have been stabilizing selection on the frequency components of the calls, but directional selection on the temporal structure (*cf* Gerhardt 1994).

Call type 1 may function to attract females (*cf* Littlejohn 1957; Gerhardt 1994) as this call type was produced more often than any other. We have no basis to suggest a function for call types 2 and 3, but the series of pulsed calls described here may represent a graded set of signals. Graded signals have been documented in other species such as *Uperoleia* (Robertson 1984), *Rana* (Jehle & Arak 1998) and *Hyla* (Schwartz 2001) and typically appear to represent an escalation in response to decreasing distance to an opponent or female (Gerhardt & Huber 2002). For example, there is a negative correlation for *Rana nicobariensis* between duration of its advertisement call and proximity of its nearest calling neighbour (Jehle & Arak 1998). *Litoria adelaidensis* males often call from emergent vegetation (typically reeds), and accordingly the physical structure of their breeding habitat may impose a limitation to male spacing. These circumstances may favour graded interactions between males.

Call type 4 was rarely recorded and may function in male-male interactions. On other occasions, we have observed pairs of males in close proximity, on a single reed stem, making this call. However, the locations of other males when call type 4 was recorded in this study are unknown. These observations, and the rarity of call type 4, indicate that it may act as a short range "encounter" call (*e.g.* Robertson 1984; Halliday & Tejedo 1995). This conclusion needs confirmation by further observation and playback experimentation.

Studies designed to further investigate the functions of the call types of *L. adelaidensis* are required. These need to examine responses of both males and females to call playback, and account for how the intensity of the calls of neighbours and male size may affect calling tactics (*e.g.* Robertson 1984; Rose & Brenowitz 1997; Brenowitz & Rose 1999). The slender treefrog may lend itself to studies concerned with the evolution of vocal repertoires and vocal behaviours in frogs.

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Impact of rabbits on native bush remnants

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Abstract

The value of rabbit-proof fencing in protecting both bush remnants and agricultural production from the impact of rabbits was examined in remnants of coastal heath on two farming properties in southern Western Australia. The short- and longer-term effects of confining wild rabbits within these remnants were studied by excluding rabbits from, or confining them to, experimental sites. In the short-term (*i.e.* within 10-14 months), it was difficult to demonstrate an effect of rabbit grazing except that the percentage cover of sedges and native grasses was clearly reduced in the presence of rabbits. Other negative impacts only become obvious over the longer-term ($\geq$2 years) when the percentage cover of sedges and grasses, and the abundance of seedlings and regenerating plants, were reduced as a result of grazing by rabbits. This effect was more pronounced by year 2, suggesting that the impact of even a small number of rabbits would worsen with time. The impact of rabbits was greatest during periods of peak rabbit abundance.

These findings strongly suggest that any residual rabbits within areas of fenced remnant vegetation must be removed prior to, or immediately after, fencing if the long-term viability of these bush remnants is to be maintained. If this could be achieved, then the use of rabbit-proof fencing to protect small areas of native vegetation from rabbits has some merit, particularly where the remnants have high conservation value.

Key words: rabbit, *Oryctolagus cuniculus*, native bushland, fencing, exclusion

Introduction

European rabbits (*Oryctolagus cuniculus*) have had a devastating impact on both agricultural production and wildlife conservation in Australia (Cochrane & McDonald 1966; Cooke 1981, 1987; Williams *et al.* 1995). Rabbit-proof fencing has been used to varying extents over many years in Australia to protect agricultural enterprises from rabbit damage (Williams *et al.* 1995). However, its use for protecting areas of native vegetation from the detrimental impact of rabbits has received little attention. In Western Australia, areas of native vegetation on farms have been left uncleared, particularly where they are growing on ridges of light sandy soil which would otherwise be subject to wind erosion. This in turn has created a different problem, because such bush remnants provide ideal habitat for rabbits. Rabbits often attain relatively high numbers in these habitats, coming out to feed on, and often severely damaging, adjacent broad-acre crops and pastures. Although their impact on bush remnants in these circumstances is poorly documented, rabbits are believed to have a significant negative impact on this vegetation. Annual poisoning programs have been used to reduce the impact of rabbits on agricultural production in such situations (Williams *et al.* 1995), but this approach does not solve the problem on a long-term basis. Clearing the native vegetation is not an option because of the potential for soil erosion to occur, and also because of the need for conserving the remnant vegetation.

Intuitively, the use of rabbit-proof fencing to reduce the numbers of rabbits in bush remnants has merit. Such fences confine rabbits to areas with less nutritious food, decreasing rabbit productivity, and preventing immigration. Both these factors can result in reduced rabbit abundance within the fenced remnants. However, landcare professionals are often reticent in recommending rabbit-proof fencing because of the potential concern that any residual rabbits may cause an unacceptable level of damage to the bush remnants. This could occur either in the short-term when rabbit numbers may be relatively high immediately following the fence construction, or over the longer-term with continuous grazing by low numbers of rabbits.

This paper addresses some of these issues, and examines whether (1) there were any short-term initial effects of confined rabbits on native bush remnants over the first year after enclosing a remnant with rabbit-proof fencing, and (2) there were any long-term effects on the vegetation (over >2 years) from a relatively low number of rabbits being confined within fenced bush remnants. We also comment on the benefits and costs of the construction of rabbit-proof fences for crop and pasture protection, and for the protection of bush remnants.

Methods

The study was undertaken in coastal mallee heath situated on two farming properties (Parsons' & Tomlinson's) near Boxwood Hill in southern Western Australia. Boxwood Hill is approximately 50 km due west of Bremer Bay. The sites used in the study had not

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been burnt for at least 12 years, and probably for much longer than this. Climate is typical Mediterranean with an annual average rainfall of 514 mm. Monthly rainfall records were obtained from the closest official Bureau of Meteorology rainfall recording station 009865 at Warra Jarra, AMG reference zone 50, 673303E 6191882N. Warra Jarra is approximately 3.5 km from the Tomlinson's site and 8 km from Parsons'. Annual rainfall during the trial period was 447 mm in 1999, 441 mm in 2000, and 598 mm in 2001.

Short-term effects of rabbits after fence construction

A 10.5 ha (350 x 300 m) patch of native mallee-heath vegetation on Parsons' property was used to determine the short-term effects of confined rabbits on remnant vegetation (Experiment 1). The impact of rabbits on the remnant vegetation was assessed, as described below, within each of thirty 10 x 10 m plots, 15 in each half of the site. The site was then divided into two halves and we surrounded one half with a rabbit-proof fence (Fig 1). At the same time, we also surrounded five of the 10 x 10 m areas (chosen at random) in both the treatment and experimental control areas with rabbit-proof fencing to exclude rabbits. These exclosures were equivalent to removing the effect of rabbits on the vegetation completely and thus enabled comparison with and without the effects of rabbit grazing. The remaining open (*i.e.* subject to 'normal' rabbit grazing) 10 x 10 m plots (10 in each of the fenced and unfenced areas) enabled the comparison to be made between the areas where rabbits were confined and where they had ready access to surrounding pastures and crops (*i.e.* 'rabbits free to move out'). Vegetation assessments, as described below, were repeated at fixed marked positions at two-monthly intervals for the 14 months immediately after the treatment vegetation was fenced.

Because the treatment in the comparison 'rabbits confined' versus 'rabbits free to move out' was the erection of the external rabbit-proof fence, the open plots (vegetation assessment areas) did not provide true replication, and so the experiment was not suitable for strict statistical analysis. However, this experiment was carried out because information about the initial effect of rabbits is critical in the decision making process about the overall effects of the rabbit-proof fencing, and the documentation of the process was valid, even without rigorous statistics. Means (± standard error) for each vegetation parameter were calculated and plotted for each monitoring period.

Long-term effects of rabbits on remnant vegetation

The long-term effects on vegetation of rabbits confined to bush remnants (Experiment 2) was assessed at two sites (*i.e.* patches of native vegetation) situated on the Tomlinson's "Pallinup Park" property. One site ("Site 1"; 11 ha; 550 x 200 m) had been rabbit-proof fenced 4-5 years previously, and the other ("Site 2"; 8.5 ha; 500 x 170 m) had been similarly fenced less than a year previously. Within each of these sites, 10 locations were randomly selected. At each location, an area of visually uniform vegetation was chosen, and in each of these a 10 x 10 m exclosure was constructed (preventing rabbit access) and a 10 x 10 m open plot, where rabbit access was unimpeded, was marked. In all exclosures and open plots, the vegetation was assessed within five 1 m² quadrats as described below. Assessments were made before the exclosures were constructed in 1999, and again at the same time of year in 2000 and 2001 once the 10 m x 10 m exclosures had been erected.

In this assessment, the exclosures constituted the treatment, so on each site there were 10 replicates, and the data were analysed by analysis of variance (Zar 1984). The analysis of variance for each measurement compared the grazed and ungrazed plots in 2000 and 2001 using the measurements from 1999 as a covariate. A split plot analysis of variance was used with the year as the sub-treatment. Residual plots were used to check that the assumptions underlying the analysis of variance were valid. Analysis of variance was also used to compare grazed and ungrazed plots in 1999, prior to any treatment effects. These analyses were made using Genstat (v 6, Lawes Agricultural Trust, Rothamsted).

Vegetation Measures

A point quadrat method (36 points; Gilfillan 1999) was used for assessing percentage cover within 10 m x 10 m permanently marked, randomly selected, plots (n = 5-10) within each of the study sites. Each plot contained five permanently marked 1 m² quadrats. One quadrat was located near each corner, and the fifth quadrat was situated in the middle, of each 10 m x 10 m plot. Care was taken to avoid edge effects caused by the fence construction and any perching birds. The following vegetation measures were taken for all quadrats: percent cover of small (<0.5 m high) understorey shrubs (SS), percent cover of sedges and grasses (SG), percent cover of other monocotyledonous plants (OM), number of quadrats (n = 5 per plot) in which seedlings or reshoots of rootstocks were visible (SR Quadrats; score, 0 (none present) to 5 (present in all 5 quadrats), and an abundance index of seedlings and reshoots combined as single category (SR Score: 1 = 1-5 seedlings/reshoots, 2 =

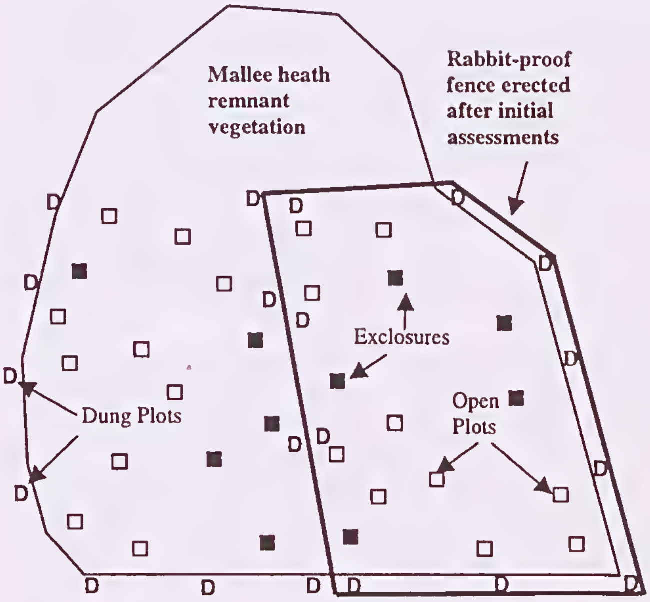
Mallee heath remnant vegetation
Rabbit-proof fence erected after initial assessments
Exclosures
Open Plots
Dung Plots
D

Figure 1. Schematic representation of the experimental design for the short-term study undertaken at the Parsons' site.

6-10, 3 = 11-20, 4 = 21-30, 5 = 31-50, 6 = 51-100, 7 = >100). The height (m) and cover (%) of the dominant (overstorey) shrub layer was also visually estimated for each 10 m x 10 m plot.

Rabbit abundance index (RAI)

Indications of the numbers of rabbits, and changes in rabbit abundance, were obtained as a rabbit abundance index (RAI) by counting rabbit dung on permanently marked quadrats. The dung quadrats were located near each open plot within the fenced and unfenced areas of the remnant vegetation in both experiments. In addition to these, dung quadrats were also positioned around the perimeter of each experimental area (see Fig 1). The number of dung pellets was counted on these quadrats every time that the associated vegetation plots were surveyed. There were 20 dung quadrats in each area of Experiment 1 and 30 quadrats in each area used in Experiment 2. The quadrats comprised 1 m^2 of bare soil (sand), and they were brushed clean after each count.

Benefits and costs of rabbit-proof fencing

To demonstrate the benefits and costs associated with the erection of rabbit-proof fencing to farmers and other landholders, areas of crop lost to rabbits were estimated by physically measuring the area affected on foot and/or by vehicle in areas where rabbits had ready access to paddocks. Production losses were calculated from the paddock yield per hectare and the current price (2001, Australian $) at 'harvest'. The cost of erecting the rabbit-proof fences was also determined.

Results

Short-term effects of rabbits on remnant vegetation

The numbers of rabbits in the fenced and unfenced areas were similar, and low, at the time the fence was constructed (Fig 2). Rabbit numbers in the fenced vegetation, as measured by the RAI, remained low throughout the experiment. However, in the unfenced vegetation there was a considerable rise in the dung counts in November which corresponds with the end of the breeding season when independent sub-adult rabbits are most abundant. The RAI suggests that rabbit numbers outside the fence rose to about five times those within the fenced vegetation. From then until the end of the experiment in July 2001, rabbit density in the unfenced area was always considerably higher than in the fenced vegetation with the confined rabbits (Fig 2).

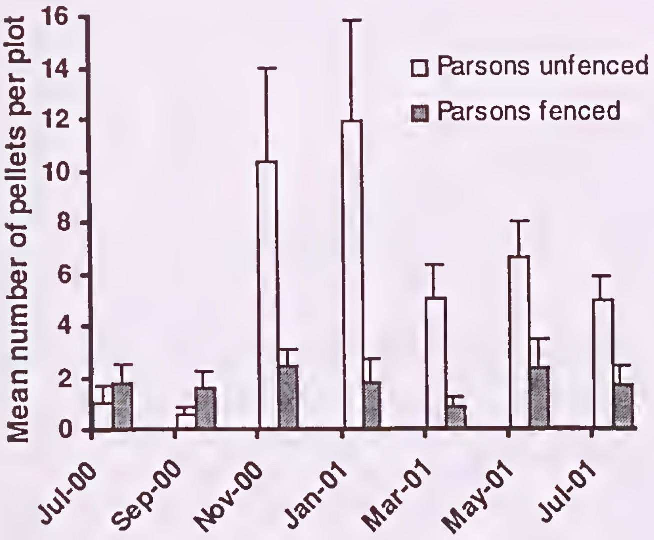

Figure 2. Changes in the rabbit abundance index (mean dung pellets per plot) for the fenced and unfenced areas of remnant vegetation during the investigation of the short-term effects of confined rabbits. Data are mean (± se) of the number of pellets per 1 m^2 quadrat (n = 20).

The overall seasonal pattern in the numbers of seedlings and reshoots (*i.e.* re-sprouting vegetation) observed in the exclosures and open plots at Parsons' site was similar between the fenced and unfenced areas (Fig 3). There was a rise in the abundance of this vegetation class in July, followed by a decline to extremely low levels in summer (January to March), and a sharp rise between May and July following the late break of season. There were, however, some differences in the detail of this response that are worthy of note. The most marked decline in the numbers of seedlings and reshoots occurred in the open plots in the unfenced vegetation between September and November. This corresponds with the considerable rise in rabbit density between the same sampling times (Fig 2). In January, when the numbers of seedlings and reshoots were declining to low levels, the open plots on both the fenced and unfenced areas showed significantly lower numbers of seedlings and reshoots than in the fenced exclosures, where rabbits had no access to the remnant vegetation. It is interesting to note that on the unfenced area, the rise between May and July was similar to the rises in the fenced area, and to that which occurred within the exclosures. This was in spite of the continuing higher levels of rabbit density as indicated by the dung counts (Fig 2). It must be remembered, though, that the rabbits in the unfenced area also had access to annual species growing in the open paddock surrounding the site.

Changes in the percentage vegetation cover of the sedges and grasses vegetation class over time, with and without confined rabbits, were similar throughout the experiment, with one exception (Fig 4). The increase in the amount of sedges and grasses seen between September and November (Spring growth) in the exclosures and in the open plots on the fenced area, was not seen in the open plots on the unfenced remnant vegetation where grazing by rabbits was unrestricted. Interestingly though, the effect on sedges and grasses did not appear to continue through January although the number of rabbits on the unfenced area remained relatively high during this period (Fig 2).

There was also a decline in the percentage cover of sedges and grasses on all open plots and in most exclosures between May and July 2001 (Fig 4). The biggest decline was in the open plots with unrestricted rabbit access within the fenced area. In the previous year, sedges and grasses had been increasing at this time of year. The decrease in the sedge and grass cover between May 2001 and July 2001 possibly reflect the later on-set of autumn rains in 2001 in comparison to 2000.

Changes in the percentage cover of small shrub category had the same seasonal trends as reported above for the other vegetation classes. There was no change in

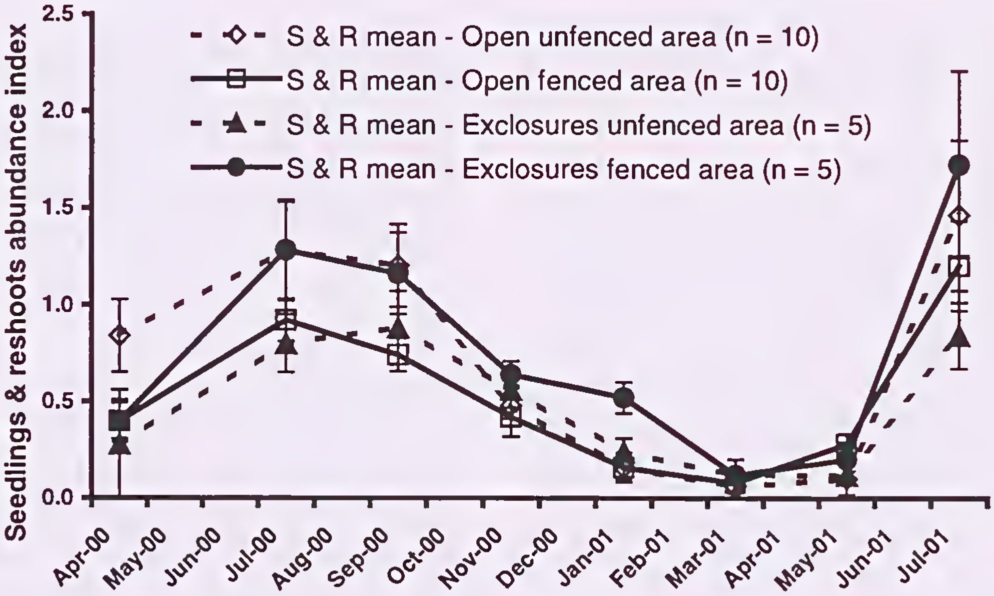

Figure 3. Changes in the abundance index of the seedlings and reshoots category as a result of rabbit grazing within fenced and unfenced areas of remnant vegetation at Parsons' site. An abundance index scale of 1 to 7 was used to score the 5 quadrats within each plot (see methods). Values are mean (± se) of the abundance index scores for the plots in each area.

the tall (over-storey) shrub category during the trial period. Rabbits would not be generally expected to have a severe short-term impact on small and tall shrubs unless rabbit densities were very high.

Long-term effects of rabbits on remnant vegetation

At the start of this experiment in 1999, there were no significant differences in the vegetation parameters measured between the exclosure (ungrazed) and the open (grazed) plots. The resulting *P*-values for the comparison between ungrazed and grazed plots were; shrub height, 0.144; shrub density, 0.206; cover – small shrubs (SS), 0.977; cover – sedges and grasses (SG), 0.917; other monocotyledonous plants (OM), 0.353; seedlings and reshoots – quadrats, 0.154; seedlings and reshoots – score (square root transformation), 0.204. This indicates that the variety and abundance of the plants were similar in these plots before the rabbit-proof fence was erected to exclude rabbits from the exclosure plots.

There were no significant differences in shrub height or density between the ungrazed and grazed plots over the two years of measurement after the erection of the rabbit-proof fences to exclude rabbits from the ungrazed plots. However, there were some interesting differences for many of the other vegetation measurements taken. The ANOVA used was a split plot design with a blocking factor (the two sites, df = 1), and with the corresponding 1999 pre-treatment levels used as a covariate. This approach did not test for differences between sites as the main interest was in the response of the remnant

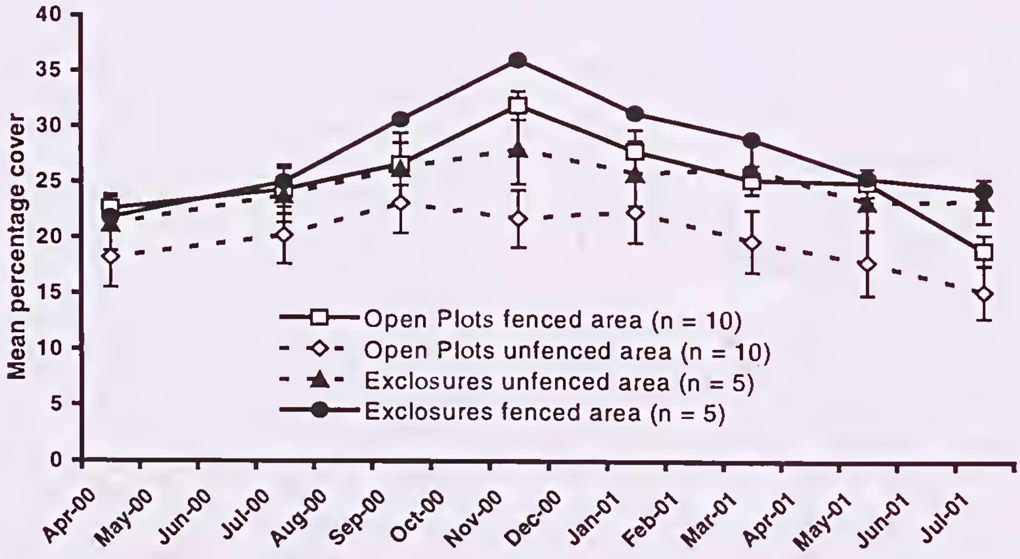

Figure 4. Changes in the percentage cover of the sedges and grasses category as a result of rabbit grazing in the fenced and unfenced areas of remnant vegetation at Parsons' site. The results from rabbit exclosure plots are included for comparison. Values are mean (± se) percentages of these plants in the plots at each area.

Table 1

Analysis (ANOVA) of the differences between the ungrazed (exclosure) and grazed (open) plots over the two year 'experimental' period. SS, small shrub cover; SG, sedge and grass cover; OM, other monocotyledonous plant cover; SR-Quadrats, number of quadrats with visible seedlings or reshooting rootstocks; SR-Score, seedlings and reshoots score without square root transformation. Significant P values are in bold.

	Probability			Treatment means			Year means		
Category	Treatment	Year	Treatment x Year	Exclosure	Open	5% LSD critical values[A]	2000	2001	5% LSD critical values[A]
SS	0.460	0.035	0.802	0.177	0.184	0.021	0.189	0.173	0.015
SG	**<0.001**	**<0.001**	0.094	0.428	0.354	0.024	0.435	0.346	0.019
OM	0.811	0.440	0.699	0.009	0.008	0.006	0.008	0.009	0.003
SR Quadrats	0.060	0.004	0.468	3.55	3.03	0.541	2.93	3.65	0.484
SR Score (No transform)	**<0.001**	**<0.001**	0.507	6.05	4.35	0.726	4.45	5.95	0.755

[A] The difference between each 'pair' of means for each parameter needs to be greater than the 5% LSD value to be significant at the 5% level.

vegetation with and without rabbit grazing (*i.e.* the treatment). However, the analyses did remove any differences between sites (block stratum), and between the 20 locations (plots) at each individual site (block.pair stratum) before examining the effects of treatment (ungrazed *vs* grazed) and year (2000 *vs* 2001). The covariate (*i.e.* the 1999 pre-treatment levels) was significant ($P < 0.05$) for all of the plant parameters tested. This indicates that the response of the vegetation in 2000 and 2001 was related to the amount and species diversity of the remnant vegetation at the start of the experiment in 1999. Thus, the use of the covariate 'compensates' for this relationship so that only the treatment effects are compared (Zar 1984).

Rabbit grazing had a significant impact upon the sedges and grasses, and on the abundance of seedlings and reshoots (treatment effect; Table 1). This effect was also greater in Year 2 as the year effect was significant for these two vegetation parameters (Table 1). However, although the magnitude of this change varied between years, the overall trends were the same in both years as none of the interactive terms (treatment x year) were significant (Table 1).

Changes in rabbit abundance throughout the long-term trial, as indicated by the RAI, are given in Fig 5. Rabbit numbers on Site 2, the area that had been fenced approximately 1 year prior to the experiment, were moderate and generally constant throughout apart from the higher numbers during the breeding season (spring/November). In contrast, rabbit numbers were lower on Site 1, the area that had been fenced for approximately 4-5 years. Although rabbit numbers were similar between the two sites at the commencement of the trials, the seasonal breeding peak in numbers, as determined by the RAI, was almost absent on Site 1 in subsequent years (Fig 5).

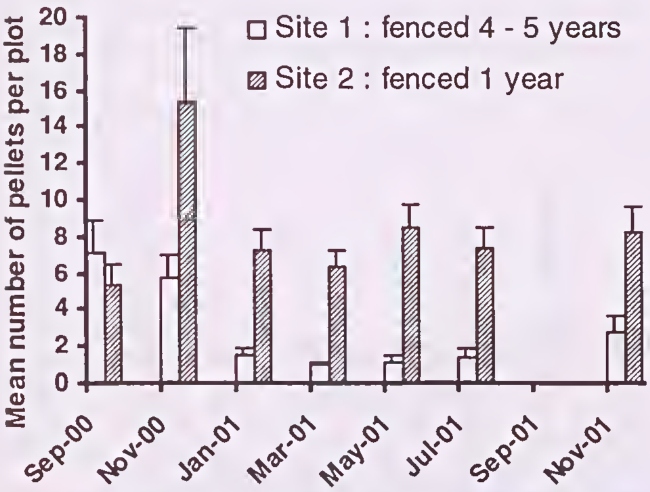

Figure 5. Changes in the rabbit abundance index (mean dung pellets per plot) for the fenced and unfenced areas of remnant vegetation during the investigation of the longer-term effects of rabbits being confined within this vegetation. Values are mean (± se) of the number of pellets per 1 m² quadrat (n = 30). Sites 1 and 2 had been fenced for approximately 4-5 years and 1 year respectively, prior to the experimental plots being established (*i.e.* when the twenty 10 m x 10 m exclosures were fenced).

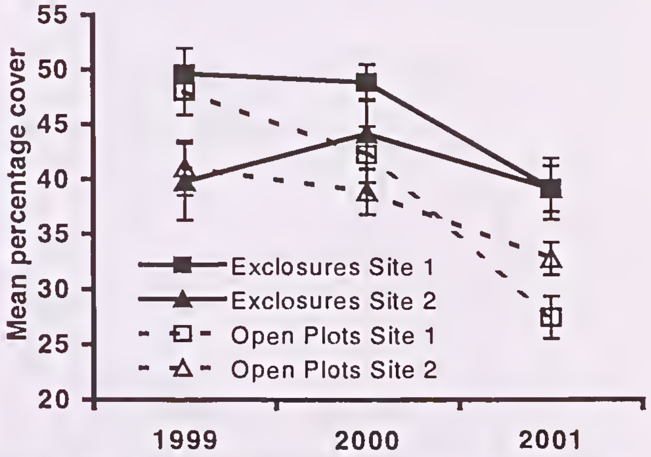

Figure 6. Changes in the percentage cover of the sedges and grasses category as a result of rabbit grazing in the fenced and unfenced areas of remnant vegetation at Tomlinson's site. Results from rabbit exclosure plots are included for comparison. Values are mean (± se) percentage cover of these plants in the 10 plots at each site. Sites 1 and 2 had been fenced for approximately 4-5 years and 1 year, respectively prior to the experimental plots being established.

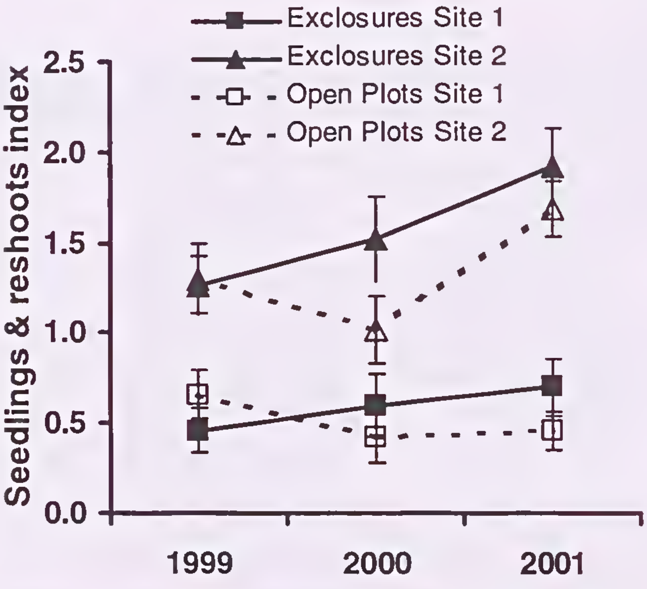

Figure 7. Changes in the abundance index for the seedlings and reshoots category as a result of rabbit grazing in the fenced and unfenced areas of remnant vegetation at Tomlinson's site. The results from rabbit exclosure plots are included for comparison. An abundance index scale of 1 to 7 was used to score the 5 quadrats within each plot (see methods). Values are mean (± se) of the abundance index scores for the plots (n = 10) at each site. Sites 1 and 2 had been fenced for approximately 4-5 years and 1 year respectively, prior to the experimental plots being established.

The main effects of rabbit grazing on remnant vegetation when rabbits were confined within this vegetation are shown in Figs 6 and 7. The ANOVA (Table 1) showed that both rabbit grazing and time (*i.e.* years) had a significant effect on the percentage vegetation cover for sedges and grasses (Fig 6). Although the abundance of sedges and grasses in the open plots and exclosures on each site were similar when the experiments were commenced in 1999, there was a consistent divergence over time between the ungrazed and grazed plots on both sites. This was presumably due to the cumulative effects of rabbit grazing, as percentage cover on the open plots was markedly reduced compared with the amount of vegetation within the ungrazed exclosures. This effect appeared to become more pronounced over time as there was a clear difference between years (Table 1). However, initially, there was little overall change in the percentage cover of sedges and grasses between 1999 and 2000, but there was a marked decline in this vegetation parameter between 2000 and 2001. This change may well have been 'driven', at least partially, by rainfall events. The period between November 2000 and November 2001 had much less rain than the corresponding period in 1999-2000 (Fig 8). In fact, rainfall over the 10 months between September 2000 and June 2001 was also considerably less than the long-term average for this period.

The seedling and reshoots score (= abundance index), and the number of quadrats with seedlings and re-shooting rootstocks, also showed a significant effect of both year and exposure to rabbit grazing at both sites (Table 1; Fig 7). Like sedges and grasses, changes in these parameters almost certainly reflected recent preceding rainfall (Fig 8). However, in the absence of grazing by rabbits (*i.e.* in the exclosure plots; Fig 7) there was an increase in the percentage cover of the seedlings and reshoots from year to year. Grazing by rabbits diminished the numbers of seedlings and reshoots, with the biggest effect occurring in November 2000 after two months of very low rainfall. As indicated by the RAI, this period also corresponds with the observed peak in rabbit abundance (Fig 5). The impact of rabbit grazing is also clearly illustrated in Fig 9 which shows the effect of even low numbers of rabbits within the fenced bush remnant (~ 5 ha^{-1}) compared to the surrounding pasture with no/few rabbits.

Costs of rabbit-proof fencing

Although the overall area of crops and pasture that was affected by rabbit grazing in the absence of rabbit-proof fencing was often small, there was usually a total loss of plant biomass in the affected areas. In canola crops, these losses ranged from $288 to $1296 (mean $972,

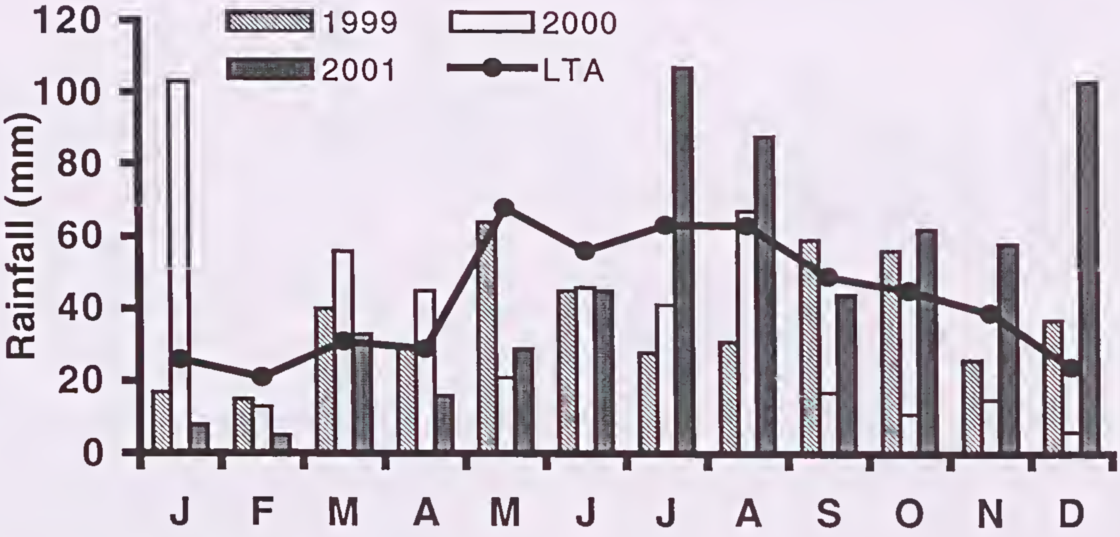

Figure 8. Long-term average (LTA) rainfall (mm), and rainfall (mm) for each of the years during the short- and long-term studies at Boxwood Hill. The recording station was within 8 km of the study sites.

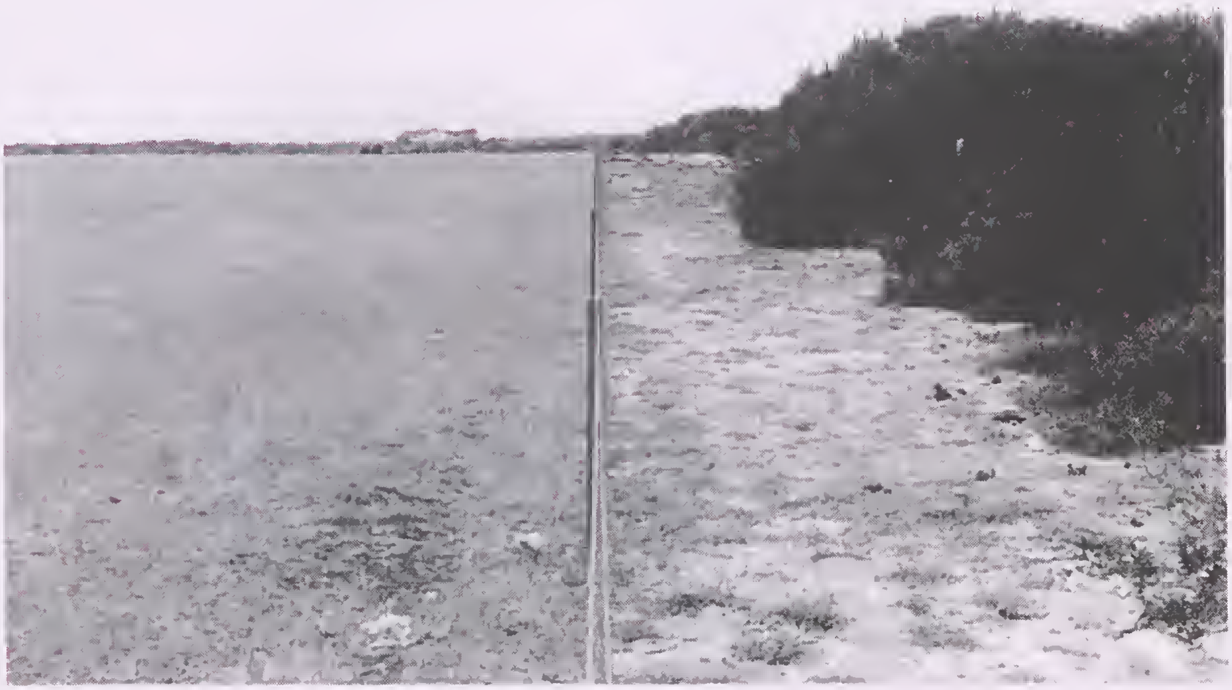

Figure 9. The clear 'rabbit-graze line' within the bush remnant (with rabbits) behind the rabbit-proof fence compared to the lack of impact in the surrounding pasture with no rabbits.

n = 4) with 0.5 ha to 3 ha (mean 1.75 ha) of crop lost. Losses were lower in lupin crops during the study, and ranged from $50 to $297 (mean $195, n = 3) or 0.25 ha to 1.5 ha (mean 0.98 ha) of affected crop. Obviously, rabbit-proof fencing is relatively permanent, and if properly maintained is likely to last for at least 15 years. Thus the associated costs would need to be discounted against the benefits obtained over such a time period. There are also tax benefits (*e.g.* depreciation) to landholders. The fence cost approximately $5 000 per km (materials, $4 000; labour, $1 000), and there is also a small on-going maintenance cost. Depending upon the shape and size of the area protected, the use of rabbit-proof fencing would cost between $250 and $500 per hectare of protected 'crop' in the first year (2001 $AUD). However, this outlay would be discounted in subsequent years.

Discussion

Short-term effects of confining rabbits

The abundance of rabbits within the fenced vegetation was always considerably less than that which occurred within the unfenced bush remnant. The dung counts in November 2000 (end of breeding season), for example, indicated a relatively large increase in rabbit numbers in the unfenced remnant vegetation which was not seen in the fenced remnant. This suggests that the rabbits within the fenced vegetation only had access to less palatable/nutritious native vegetation and this may have restricted their reproductive output. Conversely, rabbits in the unfenced remnant vegetation had ready access to a canola crop of higher nutritional value potentially enhancing their reproductive output. Significant breeding by rabbits depends on the provision of green feed of adequate nutritional quality (King & Wheeler 1985; Williams *et al.* 1995; Twigg *et al.* 1998). In the unfenced remnant vegetation, where the increase in rabbit numbers occurred, there seemed to be a greater decline in the abundance of seedlings and reshoots (re-sprouting vegetation). This was accompanied by a decline in the percentage cover of sedges and grasses that was in contrast to the fenced area, where the percentage cover of sedges and grasses had increased.

The number of seedlings and reshoots was similar between the open (grazed) and exclosure (ungrazed) plots within fenced and unfenced remnant vegetation after the 14-month monitoring period (Fig 3). There are four possible causes for this similarity, and these are not necessarily mutually exclusive. Firstly, rabbit numbers within the fenced vegetation were low and may have been below the threshold level required to cause obvious environmental damage. Conversely, because the rabbits in the unfenced remnant vegetation had ready access to other foods (eg crops and pasture), there may not have been a great demand for these rabbits to feed within the remnant vegetation as they always had access to an adequate food supply within the surrounding paddocks. Hence their impact on the remnant vegetation was minimal. This may occur irrespective of rabbit density. Thirdly, the seed bank/species richness of the remnant vegetation was depauperate, and hence the vegetation was unable to respond. We do not favour this option as our study sites had a diverse range of plant species, and we did observe a difference in the response between the exclosures and the open plots in the long-term experiment. Finally, because the numbers of rabbits ultimately confined within the fenced remnant vegetation were relatively low, it could take several years before any detrimental impacts become obvious. We believe the latter is an important consideration and that the fencing of remnant vegetation should include a strategy (*e.g.* 1080-baiting; see Williams *et al.* 1995) to reduce rabbit numbers prior to totally enclosing a bush remnant.

The short-term response of remnant vegetation following the rabbit-proof fencing appeared to be mixed. The positives mainly resulted from keeping rabbits out, which helped to maintain the confined rabbit population at low levels. However, there did appear to be some deleterious effects due to the confinement of rabbits, such as a decrease in the percentage cover of sedges and grasses.

Longer term effects of confining rabbits

Although there was a significant effect between years (the two years were markedly different in rainfall during the growing season), there is no doubt that low numbers of confined rabbits (*e.g.* ~ 5 ha^{-1}) had a significant impact on fenced remnant vegetation. In particular, the abundance of seedlings and reshoots was reduced, and sedge and grass cover was diminished, relative to the exclosures in the corresponding 1-year and 5 to 6-year fenced remnant vegetation. Given that this effect occurred within 3-7 years from when the fences were originally erected (*e.g.* for 1 year plus 2 years of experimentation), then the long-term implication is that a substantial change in the biomass and composition of bush remnants is a likely consequence of confining even low numbers of rabbits within these remnants. It is possible that some of the deleterious effects of rabbit grazing may be exacerbated by environmental stress. That is, such effects may not become obvious until the fenced remnant vegetation undergoes an additional source of abiotic stress, such as below average rainfall.

It is also noteworthy that our findings are consistent with those of other studies, and some examples of this are presented below.

- Rabbits will often selectively browse seedlings of certain shrubs and trees. In fact, there may be no 'safe' rabbit density for some tree and shrub seedlings (Morris 1939; Lange & Graham 1983). For example, with free-ranging, unconfined populations, even rabbit densities of around 4 ha^{-1} can prevent the regeneration/replacement of some plant species, particularly in arid Australia, and this can lead to significant soil erosion (Cooke 1981, 1987; Foran *et al.* 1985).
- Rabbit-grazing can also impact on native grasses, and when rabbits are excluded, native perennial grasses will regenerate and rapidly replace many of the introduced annual grass species (Mallet & Cooke 1986).
- In some sub-alpine areas, the effects of rabbit-grazing resulted in the loss of nine palatable forbs within seven years. However, where rabbits were excluded there was a net overall gain of two species (Leigh *et al.* 1987). The presence of rabbits led to a substantial reduction in the cover, biomass and species diversity of the forbs in this habitat.
- In the Victorian mallee district, seventeen native species of ground-layer plants were recorded where rabbits had been excluded for two years but none of these plant species were found where rabbits had ready access to such areas (Cochrane & McDonald 1966).

These findings, and the results of our study, strongly support the need for a strategy for reducing the numbers of rabbits present in bush remnants prior to the remnant vegetation being totally enclosed with rabbit-proof fencing. This could be achieved by a well conducted baiting program, preferably with 1080, which may or may not need to be integrated with a shooting program to mop up any remaining rabbits. Unless rabbits are eradicated from fenced bush remnants, there will be an ongoing need to conduct regular control programs to prevent/reduce the detrimental effects of rabbit grazing.

Benefits and costs of rabbit-proof fencing

Fencing that excludes rabbits from 'prime habitat' can decrease the effects of rabbit grazing by limiting their capacity for population growth. If conducted on a sufficient scale, then this in turn reduces the number of rabbits that can potentially inflict damage to the surrounding crops and pastures. The benefits of rabbit-proof fencing can outweigh the expenditure and become cost-neutral to agricultural producers in the medium term (≥2 years). The protection gained is also long-term. With a high value crop such as canola, costs can be recovered within two seasons, depending on the amount of fencing required, and the crop yields and returns obtained. The benefit-to-cost ratio of rabbit-proof fencing to eliminate rabbit damage is likely to be even more favourable for high return horticultural crops/market garden enterprises. This is particularly so as a poisoning program does not provide the same absolute protection compared to that achieved with rabbit-proof fencing. Small crop losses may well continue to occur following a baiting program unless some technique is used to remove any remaining rabbits (*e.g.* shooting).

Implications for rabbit management and bush remnants

Provided that some means are used to reduce residual rabbits, then rabbit-proof fencing of remnant vegetation of high conservation value would be well worthwhile. Obviously the benefits and costs depend on the size of the area that needs to be protected. Nevertheless, we do have some caveats. In the short term (one year), the effect of confining rabbits within remnant vegetation, thereby reducing available rabbit habitat, may be both positive and negative. Such effects were not always easy to define. However, based on the results of our longer term experiment, the effect of confining rabbits within bush remnants over a much longer term (say, 15 years) will almost certainly be negative unless steps are taken to remove the residual rabbits completely (*i.e.* eradication is achieved). This would be quite achievable using a combination of poison baiting and shooting, particularly if control efforts were undertaken when other food is in relative short supply (*e.g.* during summer). If the long-term viability of the remnant bush is to be maintained, then every effort needs to be made to ensure that residual rabbits are completely eradicated. If this is not achieved, then the bush remnants themselves may need to be subjected to regular poisoning campaigns, in addition to the cost of the fence, to prevent the deleterious effects caused by residual rabbits. Such a situation may well be little better (or possibly worse) than employing a regular poisoning program, without the fence, to reduce the impacts of rabbits.

One potential negative impact of using rabbit-proof fencing to protect bush remnants is that it may interfere with the movement of native animals, particularly kangaroos and wallabies. The conservation issues potentially associated with this may be important if species of high conservation value, or species that are under threat, are involved. How important this is may need to be balanced against the losses inflicted to crops and pasture, the potential loss of native vegetation, and the conservation value of the vegetation of concern. Such issues will need to be considered carefully on a case by case basis.

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New record of siliceous, marine, later Eocene from Kalbarri, Western Australia

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Abstract

Weathered residue of a previously undetected thin Eocene unit at elevation of 220 m AHD east of Kalbarri includes silicified sponge-rich calcarenite and argillite. Sponges (intact forms and spicules) dominate the silicified fauna but common smaller benthic and planktonic foraminifers, molluscs (gastropods, bivalves, scaphopods, and nautiloids), bryozoans, solitary corals, and serpulid worms are also present. The planktonic foraminifers indicate that the unit lies within the Zone P13 to P16 interval of the Middle to Late Eocene (40.5 – 34.0 Ma BKSA95). In comparison to the Giralia Calcarenite of upper Zone P12, the fossil assemblage indicates that significant cooling in the shallow inner neritic zone apparently took place within the basin during the later Eocene. The ages of known marine Eocene occurrences in the basin, and the contrast between these and underlying formations, indicate major erosion during the interval 53 – 41.5 Ma (late Early to early Middle Eocene) preceding deposition of Zone P12–16 units.

Key words: siliceous, Eocene, Kalbarri, sponges, foraminifers, molluscs, South Carnarvon Basin

Introduction

The marine Eocene in mainland Australia is best known from the southern margin of the continent (McGowran *et al.* 2000; Li *et al.* 2003). Outcrops of such strata in the Southern Carnarvon Basin have been recorded only north of about 26 °S (Fig 1; Haig *et al.* 1997), and have been placed in two formations, the Giralia Calcarenite and the Merlinleigh Sandstone (Condon 1968; Hocking *et al.* 1987). Based on planktonic foraminifers, Haig *et al.* (1997) correlated the lower part of the type section of the Giralia Calcarenite to the upper part of Zone P12 of Berggren & Miller (1988), of Middle Eocene age (about 41.5 – 40.5 Ma according to the BKSA95 time-scale of Berggren *et al.* 1995). Haig *et al.* (1997) interpreted the entire formation at the type locality as the upper transgressive and lower highstand systems tract of one sequence, and suggested that this section represents a limited time interval. Outcrops of the formation at Red Bluff (north of Carnarvon) and Yaringa were correlated with the type section, as was the Merlinleigh Sandstone, although on much more tenuous evidence. Brunnschweiler (1962) had attributed the Merlinleigh Sandstone to the Middle Eocene (upper Cuisian or Lutetian) based on echinoids.

This paper records a new discovery of an Eocene location near the southern margin of the Southern Carnarvon Basin (Fig 1) that is younger than other Eocene localities in the basin, and contains a cooler water fauna. The locality also allows a more precise age to be placed on a major interval of erosion that affected the entire post-breakup basin. Locality details are lodged in the collection register of the E de C Clarke Geology Museum, The University of Western Australia.

Description of site and stratigraphic relationships

The locality lies 27 km east of Kalbarri at about 220 m AHD (Fig 2), and consists of scree dominated by iron-stained siliceous argillites with scattered large fragments of silicified bryozoans as well as large (up to about 30 cm) intact siliceous sponges. A relatively clean sponge-spicule dominated arenite that includes silicified calcareous skeletal grains (including abundant foraminifers, and common gastropods and bryozoan fragments) is also present. The locality extends about 2 km along a low breakaway capped by coarse-grained unfossiliferous silicified and ferrugenised pebbly sandstone probably less than 1 m thick. To the west and south, low exposures of Windalia Radiolarite are present no more than 5 m below the ferrugenised sandstone, thereby setting an upper limit for the thickness of the Eocene at this locality.

Within the scattered rubble of Eocene argillite and silicified calcarenite are pebbles of siliceous porcellinite and silicified belemnite guards (*Peratobelus*) derived from the Late Aptian Windalia Radiolarite (Clarke & Teichert 1948; Hocking *et al.* 1987; Ellis 1993; Haig *et al.* 1996), implying that the Eocene lies unconformably on this Cretaceous unit. The Eocene unit is not formally named because no *in situ* outcrop is present; only the weathered residue of the unit remains at the studied locality.

Eocene fossil assemblage and correlation

All fossils recovered from the site are silicified or were originally siliceous (*e.g.* sponges). Some of the original calcareous skeletons are chalcedonic internal moulds (*e.g.*

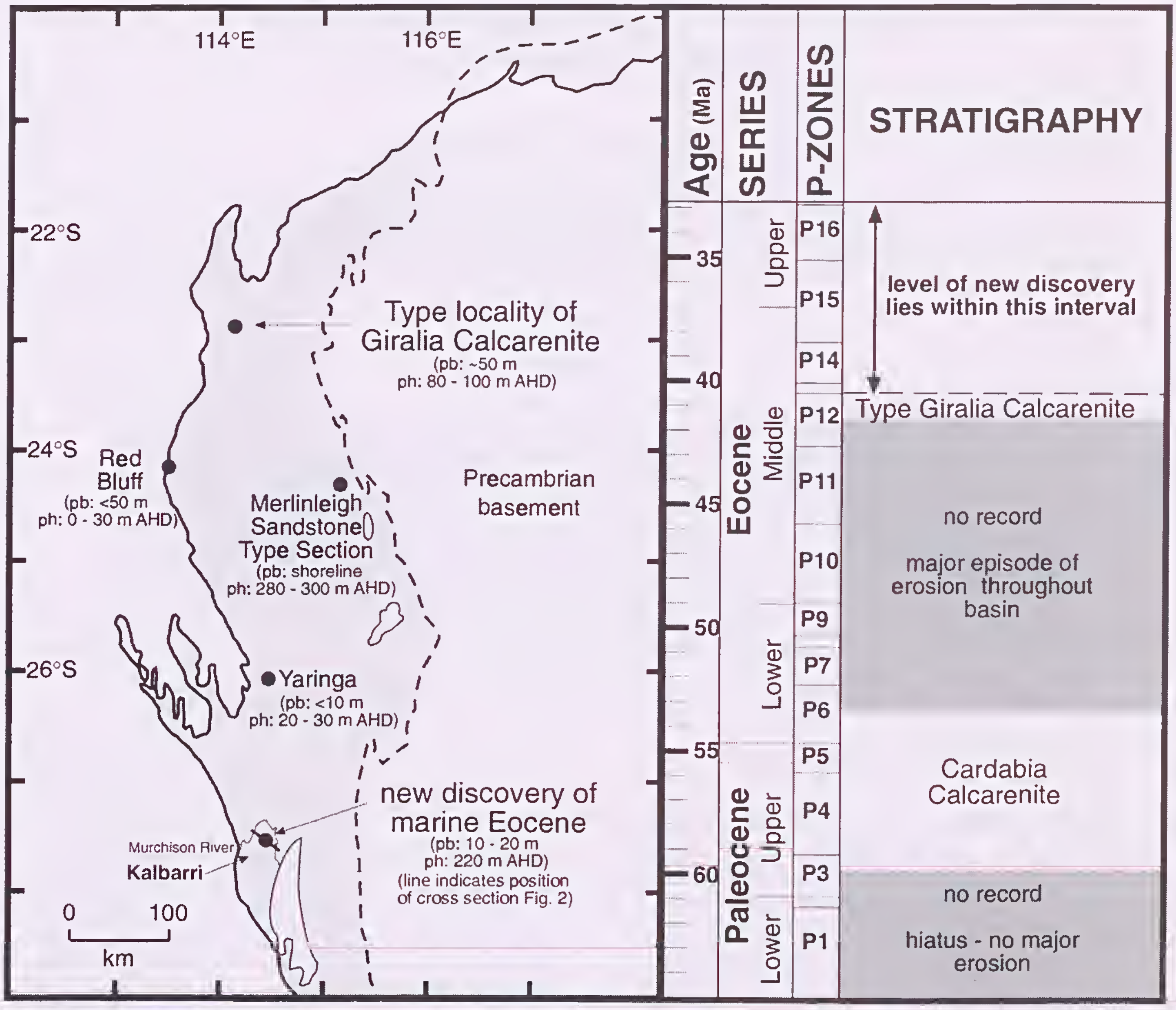

Figure 1. Known outcrop localities of the marine Eocene in the Southern Carnarvon Basin, and the stratigraphic position of the newly discovered unit with respect to other Paleocene–Eocene units known in the basin. pb = palaeobathymetry; ph = present height. The chronometry, series correlations, and P-Zones follow Berggren & Miller (1988) and Berggren *et al.* (1995).

nautiloids and some gastropods); in others the skeleton has been replaced by silica, and chalcedony has in-filled internal cavities. While silicification has preserved the overall morphology, most fine morphological details and microstructure have been lost. The rock samples show that silicification was pervasive as all carbonate grains are replaced and preserved as either casts or moulds.

Demosponges are the most abundant fossils, and are represented by well-preserved intact skeletons, up to 30 cm across, as well as spicules. Bryozoans are diverse and include encrusting types as well as fragments of free specimens. Among the molluscs are common high-spired gastropods, ornamented and smooth bivalves (most equivalved with valves intact), scaphopods, and a few nautiloids including *Aturia* sp (Fig 3Q,R) and an unidentified nautiloid with very gently curved septa (Fig 3S,T). Serpulid worms are encrusted on other macrofossils. Among the microfossils, apart from the prolific sponge spicules, foraminifers are abundant and

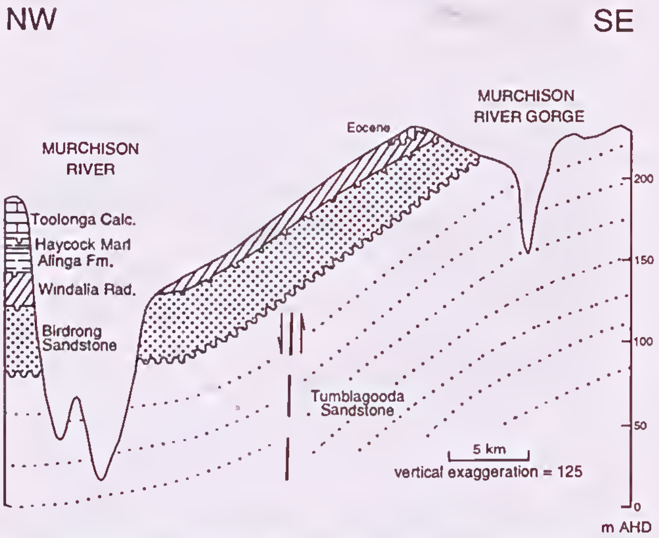

Figure 2. Schematic NW-SE cross-section through new locality showing stratigraphic relationships. The line of section is shown on Fig 1.

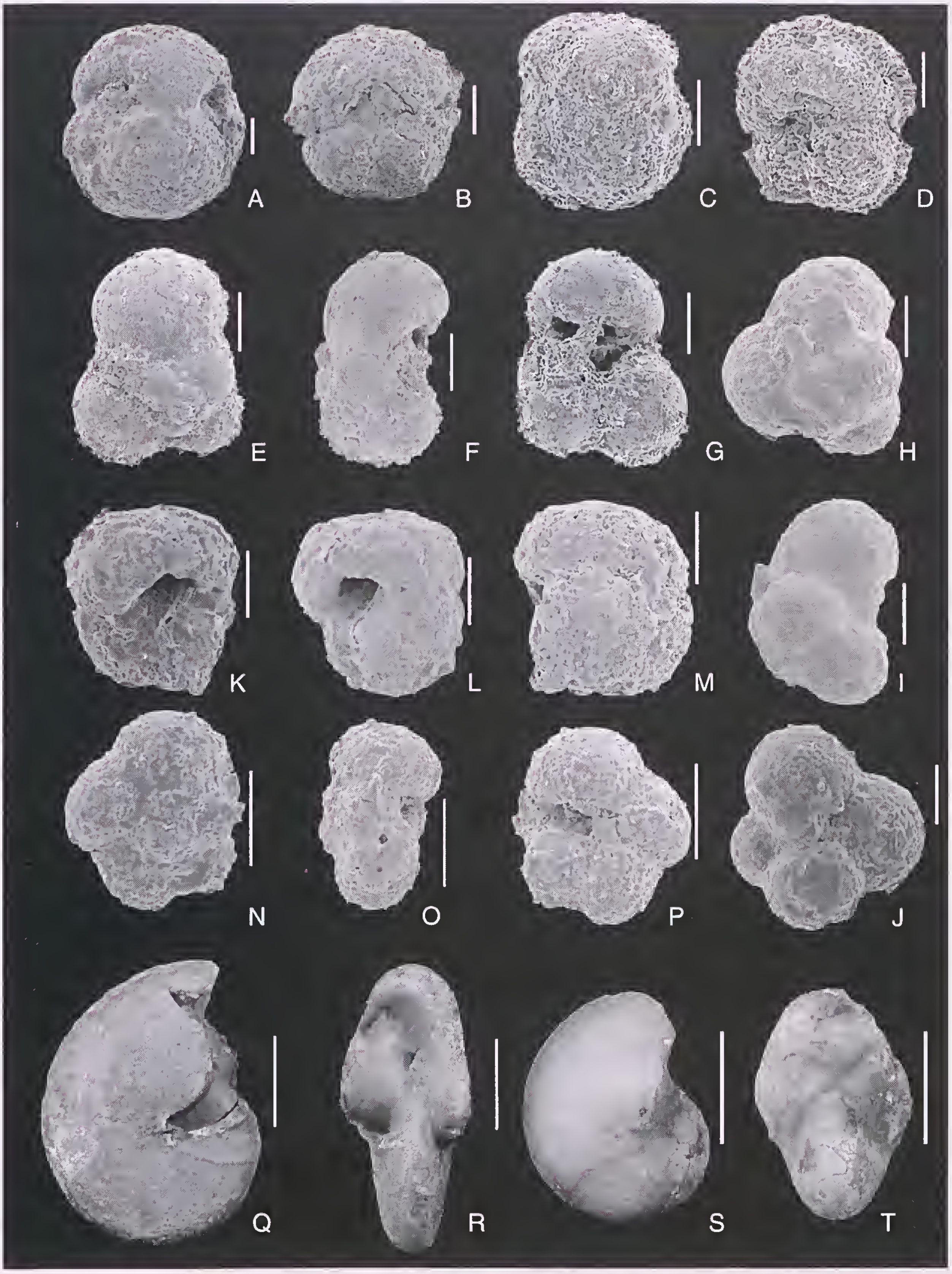

Figure 3. Key fossils for age determination, preserved as siliceous casts. A–P; Planktonic foraminifers (bar scales = 0.1 mm; secondary electron images). A, B; *Globigerinatheka index* (Finlay), lateral views of different specimens, A UWA132079, B UWA130882. C; *Catapsydrax*? sp, umbilical view with umbilicus covered by bulla, UWA130883. D; *Subbotina linaperta* (Finlay), umbilical view, UWA130884. E–G; *Subbotina inaequispira* (Subbotina), spiral, peripheral, and umbilical views of same specimen, UWA130885. H–J; *Subbotina eocaena* (Gümbel) transitional to *S. corpulenta* (Subbotina), spiral, peripheral and umbilical views, UWA130886. K–M; *Turborotalia*? sp possibly from *T. cerroazulensis* lineage, umbilical, peripheral and spiral views, UWA130887. N–P; *Acarinina*? sp, spiral, peripheral and umbilical views, UWA130888. Q–T; Nautiloids (bar scales = 1 cm); reflected light micrographs. Q, R; *Aturia* sp, lateral and peripheral views, UWA130880. S, T; nautiloid indet, lateral and peripheral views, UWA130881.

dominated by benthic types of the Orders Rotaliida (including *Cibicidoides, Gyroidinoides, Planogypsina*) and Miliolida (including *Quinqueloculina, Triloculina, Pyrgo*). Less common agglutinated foraminifers (including *Textularia*) and species of the Order Buliminida are also present. Planktonic foraminifers form about 10% of the foraminiferal assemblage. Ostracods make up a small percentage of the microfossil assemblage.

Of the fossil groups present, the planktonic foraminifers provide the best indication of age, and key species are illustrated in Fig 3. The recovered assemblage includes none of the species that define Berggren & Miller's (1988) zonation for the tropical and subtropical Eocene. However, the range charts provided by Toumarkine & Luterbacher (1985) linked to the P-zonation of Berggren & Miller (1988; rather than to the P-zones listed by Toumarkine & Luterbacher) are useful in broadly defining an age for the present material based on international criteria. *Globigerinatheka index index* is recognized by its distinctive coiling, high-arched apertures and incised sutures (Fig 3A,B). According to the compilation of Toumarkine & Luterbacher (1985), this subspecies ranges from Zone P11 to the lower part of Zone P16 (Upper Eocene) and sporadically higher to the top of Zone P17 (the Eocene–Oligocene boundary according to Berggren & Miller 1988). The presence of common *G. index index* therefore indicates that the new unit lies no higher than Zone P16. *Subbotina inaequispira* (Fig 3E–G) ranges from within Zone P7 to uppermost Zone P12. According to Berggren & Miller (1988, p 373) it may range into Zone P13. *Subbotina eocaena* ranges consistently from within P10 to the Oligocene, with descendant *S. corpulenta* ranging from the base of P13 into the Oligocene. The recovered specimens (Fig 3H–J) seem transitional between *S. eocaena* and more high-spired *S. corpulenta*, and imply that the new unit lies within or above Zone P13. The specimen illustrated in Fig 3K–M is a robust low trochospiral form with 3.5 chambers in the final whorl and with chambers elongated in the direction of coiling. The aperture seems to be a relatively high arch from the umbilicus toward the periphery. The wall is deeply corroded, but was probably coarsely perforate. It some aspects, it resembles *Acarinina primitiva* (Finlay) which ranges from the Paleocene to the top of P13 (according to Toumarkine & Luterbacher 1985) and to the 39.0 Ma BKSA95 datum level. More probably, because of its looser coiling and higher arched aperture directed more to the periphery, it belongs to the *Turborotalia cerroazulensis* lineage as outlined by Toumarkine & Luterbacher (1985). The broad peripheral margin shows that the specimen is closer to *T. cerroazulensis pomeroli* than to the more advanced *T. cerroazulensis cerroazulensis*, which has an angled periphery. According to Tourmarkine & Luterbacher (1985), *Turborotalia cerroazulensis pomeroli* is the most abundant and widespread of the subspecies of the *T. cerroazulensis* lineage and ranges through Zones P12 to P17 (Middle to Upper Eocene). Among the other planktonic foraminifers, the specimen tentatively referred to *Catapsydrax* (Fig 3C) has a distinct bulla across the umbilicus and possibly a spinose surface, and may be related to *Catapsydrax echinatus* Bolli of the Middle Eocene (following Stainforth *et al.* 1975). *Subbotina linaperta* (Fig 3D) is a long-ranging species, and the species designation of *Acarinina?* sp (Fig 3N-P) is uncertain and its generic attribution tentative.

Collectively, the planktonic foraminifers indicate that the newly discovered site belongs within the P13 to P16 zonal range (40.5 – 34.0 Ma BKSA95). The absence of zonal index species that would narrow the stratigraphic range may indicate environmental constraints. Distinctive species of *Truncorotaloides*, that are abundant in the upper Zone P12 assemblage from the type Giralia Calcarenite (Haig *et al.* 1997) and range elsewhere to the top of Zone P14, are absent from the new assemblage. *Morozovella*, which also ranges upward to the top of Zone P14, is absent from the new assemblage and from the Giralia Calcarenite P12 assemblage. Two explanations may account for the absence of these genera in the new assemblage: (1) the environment was too cool or too shallow for these genera (see discussion below on independent evidence for a cool shallow-water environment); (2) the new assemblage may belong to a level higher in the Upper Eocene than Zone P14.

Comparison with known Eocene in Southern Carnarvon Basin

The fossil assemblage from the new locality differs substantially from other Eocene assemblages in the Southern Carnarvon Basin (Appendix 1), especially as photozoan benthic faunal elements that characterize warm waters (using the definition of James 1997) are absent. These include "larger" (complex) benthic foraminifers that are abundant in the Giralia Calcarenite type section, at Red Bluff (north of Carnarvon) and Yaringa, and hermatypic colonial corals that are common in the Merlinleigh Sandstone. In contrast, sponges have not been recorded previously from Eocene localities in the basin, but are dominant at the newly discovered site. In this respect, the new unit resembles the Plantagenet Group of the Bremer and Eucla Basins on the southern margin of Western Australia (Gammon *et al.* 2000).

Because of the abundance of robust diverse miliolid foraminifers and the low planktonic percentage (about 10%), the new unit probably accumulated in inner neritic conditions (following Murray 1991), at water depths between about 10 and 30 m (based on unpublished observations of DW Haig for present-day assemblages along the Western Australian coast). This appears to be shallower than for the lower part of the Giralia Calcarenite type section (about 50 m water depth according to Haig *et al.* 1997), but deeper than for the Giralia Calcarenite at Yaringa and for the Merlinleigh Sandstone (see Fig 1). Based on the deduced water depth, the new unit should contain skeletal material belonging to groups such as larger benthic foraminifers, colonial corals, or coralline algae, if it is coeval with the Giralia Calcarenite and Merlinleigh Sandstone. Their apparent absence, however, implies that it is somewhat different in age to these units.

Discussion

The faunal composition of the new unit implies that climatic cooling in the Southern Carnarvon Basin took place during the later Eocene after about 40.5 Ma (BKSA95). McGowran *et al.* (2000) recorded a similar cooling for the later Eocene in southern Australian basins, but the foraminiferal assemblage recovered from Kalbarri does not allow a precise correlation with the southern Australian cooling events. The interregional correlations may only be confirmed by study of thicker, better preserved sections of the Eocene on the North West Shelf (see Apthorpe 1988), if continuously cored sections become available there.

The new discovery adds to knowledge of the erosion history of the basin prior to 41.5 Ma. Erosion of between 25 and 250 m of Cretaceous, and possibly also Paleocene and lower Eocene strata, is estimated to predate deposition of the shallow-water Eocene. The lower estimate is based on the thickness of the Cretaceous Alinga Siltstone and Toolonga Calcilutite preserved below calcrete on the Pillawarra Plateau 22 km north-west of the new location. The upper estimate is based on the maximum thickness of the Toolonga Calcilutite and overlying Cretaceous and Paleocene units further north in the basin. Below the type section of the Giralia Calcarenite, all units down to the Windalia Radiolarite were deposited in mid- to outer neritic settings on a broad, gently inclined continental shelf. The facies in these units are laterally uniform and, although there are hiatuses within the Cretaceous to Paleocene succession, they do not indicate major erosion even though the thicknesses of the units vary (*e.g.* see Dixon *et al.* 2003a, b).

Zones P12–P16 (including outcrops of the Giralia Calcarenite, the new unit, and the Merlinleigh Sandstone) encompass a variety of depositional settings in the Southern Carnarvon Basin (Fig 1). Sediment deposited at that time overlies lowest Eocene at the type section of the Giralia Calcarenite (Haig *et al.* 1997); Campanian (Upper Cretaceous) at Yaringa (Belford 1960); Lower Permian at the Merlinleigh Sandstone type section (Condon 1968); and Aptian (Lower Cretaceous) at the new locality. This implies a significant episode of erosion in the basin during the late part of the Early and early part of the Middle Eocene (about 53 Ma to 41.5 Ma BKSA95). The differences in present heights of the Eocene units in the Southern Carnarvon Basin (see Fig 1) are probably the result of late Neogene uplift, which also elevated underlying Cretaceous strata at the new site by about 60 m relative to the position of equivalent units on Murchison House Station, 22 km to the northwest (Fig 2).

Whatever caused the Early to Middle Eocene erosional event in the Southern Carnarvon Basin also affected the southern margin basins (as there is no record for most of this interval in southern or continental Australia, according to McGowran *et al.* 2000). Coevally, along the northern margin in the Papuan Basin and on the southern Papuan Peninsula there was a change from Cretaceous–Paleocene generally deep-water uniform calcareous mudstone facies to diverse inner neritic Middle Eocene shallow-water limestones (Haig *et al.* 1993).

The three main conclusions that arise from the new discovery are;

1) the new unit, which was deposited in the shallow inner neritic zone, represents the youngest known Eocene in the Southern Carnarvon Basin, and appears to belong within planktonic foraminifera Zones P13 to P16 of Middle to Late Eocene age (40.5 – 34.0 Ma BKSA95);
2) significant cooling within the basin apparently took place during the later Eocene after 40.5 Ma; and
3) a major episode of erosion is inferred during the 50 – 41.5 Ma interval (late Early to early Middle Eocene) preceding deposition of the Middle Eocene units.

Acknowledgements: The Western Australian Department of Conservation and Land Management is thanked for granting us permission to collect material from the newly discovered unit. We thank David Barton of Kalbarri for sharing his knowledge of the area and guiding us to the site, Tony Cockbain for alerting us to the new unit, which was assumed to be part of the Windalia Radiolarite, and Brian McGowran and Ken McNamara for improving the manuscript. Logan Barber, Ben Hammond and Rowena Pallister are thanked for assistance with drafting and manuscript preparation. AJM publishes with the permission of the Director of the Geological Survey of Western Australia.

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Appendix 1

Fossil assemblages previously recorded from the Eocene of the Southern Carnarvon Basin. Localities are shown in Fig 1.

A. Type section of Giralia Calcarenite, Giralia Anticline

"Smaller" Benthic Foraminifera: Species belonging to the agglutinated Foraminifera *Dorothia*, *Gaudryina*, *Pseudoclavulina*, *Semivulvulina*, *?Spirotextularia*, *Textularia*, *?Uvigerinammina*; Order Lageniida, *Astacolus*, *Dentalina*, *Favulina*, *Globulina*, *Guttulina*, *Laevidentalina*, *Lagena*, *Lenticulina*, *Palmula*, *Pyramidulina*, *Ramulina*, and *Vaginulina*; Order Buliminida, *Angulogerina*, *Brizalina*, *Globocassidulina*, *Kolesnikovella*, *Loxostomina*, *Reussella*; Order Rotaliida, *Alabamina*, *Amphistegina*, *Anomalinoides*, *Asterigerinata*, *Astrononion*, *Cibicides*, *Elphidium*, *Epistominella*, *?Glabratella*, *Gyroidinoides*, *Maslinella*, *?Neoeponides*, *Nonionella*, *Operculina*, *Pijpersia*, *Planorbulinella*, *Pullenia*, *Sherbornina*, *Stomatorbina*, *?Valvulineria* (illustrated by Haig *et al.* 1997)

"Larger" Benthic Foraminifera: Species belonging to Order Rotaliida *Asterocyclina*, *Discocyclina*, and *Nummulites* (Edgell 1952; Cockbain 1978); and Order Miliolida *Alveolina* (Edgell 1952)

Planktonic Foraminifera
Species attributed to upper part of Zone P12 of the Middle Eocene: *Acarinina primitiva* (Finlay), *A. senni* (Beckmann), *A. bullbrooki* (Bolli), *A. collactea* (Finlay), *A. pseudotopilensis* Subbotina, *Globigerinatheka kugleri* (Bolli, Loeblich & Tappan), *Globigerinatheka subconglobata subconglobata* (Shutskaya), *Guembelitrioides* sp. cf. *G. higginsi* (Bolli), *Hantkenina* sp *cf H. australis* Finlay, *Pseudohastigerina micra* (Cole), *Subbotina frontosa* (Subbotina), *Truncorotaloides topilensis* (Cushman), and *Truncorotaloides rohri* Brönnimann & Bermúdez (Haig *et al.* 1997)

Nautiloids
Species including: *Aturia* sp *cf A. clarkei* Teichert, *Aturoidea brunnschweileri* Glenister, Miller & Furnish; *Teichertia prora* Glenister, Miller & Furnish (Glenister, Miller & Furnish 1956)

Other skeletal debris observed in thin section (Haig *et al.* 1997)
Bryozoans; echinoids; coralline algae; *Distichoplax* algae

B. Giralia Calcarenite at Red Bluff

Benthic Foraminifera
"Larger" calcareous hyaline species (Order Rotaliida): species belonging to *Asterocyclina* and *Discocyclina* (Cockbain 1978)

Planktonic Foraminifera
Globigerinatheka and morphotypes of the *Acarinina–Truncorotaloides* complex (Haig *et al.* 1997)

Other skeletal debris observed in thin section (Haig *et al.* 1997)
Bryozoans

C. Giralia Calcarenite at Yaringa

Benthic Foraminifera
"Larger" calcareous hyaline species (Order Rotaliida): species belonging to *Discocyclina* and *Asterocyclina* (Cockbain 1978)
Other benthic foraminifera: smaller Rotaliida including *Cibicides*; rare agglutinated and buliminid species (Haig *et al.* 1997)

Planktonic Foraminifera
?Acarinina and *Subbotina* (Haig *et al.* 1997)

Other skeletal debris observed in thin section (Haig *et al.* 1997)
Bryozoans, echinoids, molluscs

D. Type section of Merlinleigh Sandstone

Benthic Foraminifera
Calcareous hyaline benthic species (Order Rotaliida): species of *Maslinella*, *Crespinina*, *Operculina*, *Rotalia* (Cockbain 1981)

Nautiloids
Aturia clarkei Teichert (Teichert 1944)

Other fossil groups
Colonial corals (species of *Cyphastrea*, and *Duncanopsammia* according to Pulley 1959); hydrozoans (*viz Millepora* according to Pulley 1959); echinoids (species of *Cyamidia* and *Lenicyamidia* according to Brunnschweiler 1962); molluscs (Condon 1968); bryozoans (Cockbain 1981); leaf fossils, teredine-bored wood, and *Banksia* fruiting bodies (McNamara & Scott 1983)

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Notes on ....

Surface activity of arid-adapted frogs

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Abstract. The arid-adapted *Neobatrachus sutor* and *Pseudophryne occidentalis* are most surface active immediately after heavy rain. The number of these frogs caught in pit-traps declined rapidly over a four day period after rain ceased. As we found no evidence of breeding, we concluded that *N. sutor* had come to the surface to feed, most probably on termites which we observed in very large numbers. We estimate the number of occasions that these two species of frogs could have been surface active, based on rainfall data, to be ≥ 9 and ≥ 17 yr^{-1} respectively.

Key words: *Neobatrachus sutor, Pseudophryne occidentalis,* frogs, abundance, activity

Introduction

Arid-adapted frogs spend most of their lives buried underground waiting for rain (Morton *et al.* 1993; Predavec & Dickman 1993; Read 1999). Some form cocoons (*e.g. Neobatrachus sutor*; Withers 1995) and others find a moist location under rocks or vegetation to minimise water loss and survive for extended periods (*e.g. Pseudophryne occidentalis*; Tyler 1994). These frogs surface immediately after heavy rain. Read (1999) reported that surface activity of *Neobatrachus centralis* in the chenopod shrubland around Olympic Dam was not restricted to rainfall events, but they were mostly found surface active after more than 5 mm of rain; *N. centralis* was active for up to 20 days after heavy rain, and disappeared just before the ponds dried out. Morton *et al.* (1993) reported that arid-adapted frogs (*Neobatrachus* spp, *Notaden nichollsi*, *Uperoleia micromeles* and *Cyclorana maini*) were most abundant immediately after heavy rains and their numbers 'tailed off' within about two days of the cessation of showers. They suggested that arid-adapted frogs do not always attempt to breed when they emerge, coming to the surface to feed and replenish energy stores in preparation for a further period of inactivity.

We report here on activity periods for *N. sutor* and *P. occidentalis* immediately after two rainfall events at Ora Banda (30° 22'S, 121° 03'E; Eastern Goldfields region) during January/February 2003.

Materials and methods

We surveyed small terrestrial fauna at four sites in the Ora Banda area. Frogs were captured in either 20 L PVC bucket pit-traps or 150 mm PVC stormwater pipes. Forty-eight pit-fall traps were arranged in eight rows of six pit-traps (alternating bucket and pipe) in the undisturbed areas. We also had 36 pit-traps in six rows of six on the sides and 36 pit-traps in six rows of six on the top of the mining waste dumps. A fly-wire drift fence joined each line of six pit traps. All pit-traps were open on the nights of 28 January to 4 February 2003. The Paddington gold mine (within 25 km of all sites) recorded 6 mm of rain on 27 January, 15 mm on 28 January, 9 mm on 2 February and 2.5 mm on 3 February. Summer thunderstorms are often very localised and rainfall can vary appreciable over a few kilometres as it did on these two occasions. Puddles and pools of water were evident along the roadside for two days after each rainfall event. Other than where runoff accumulated near the base of mining waste dumps, we found no substantial pools of water in areas not disturbed by mining activity two days after rain ceased. However, water along roadsides remained for a longer period. Night searches for frogs were undertaken on 1st and 2nd February at all four sites.

Results

Seventy six *N. sutor* and 288 *P. occidentalis* were captured during the seven nights of trapping. We found a few *P. occidentalis* in some of the larger ponds on the top of a waste dump during the day. Both species of frogs were most abundant the first night after heavy rain and the number pit-trapped rapidly declined to very low levels by three to four days after the rain ceased (Fig 1).

Having driven approximately 60 km around the study sites at night we heard only one *N. sutor* calling from a pond and a large number of *P. occidentalis* calling from a variety of locations. We saw no tadpoles in residual ponds after the rain, but the water was very coloured and visibility was very poor, so if tadpoles were in the ponds they may not have been seen. We did not search for *P. occidentalis* eggs in moist tunnels.

A large number of termite alates were observed during the build up to the first thunderstorm and on the night it first rained. We observed many swarms of termites active on the surface of logs and the leaf litter mid-morning on the first day after heavy rain.

Discussion

Arid-adapted frogs come to the surface after heavy rain for two purposes, to breed and to restore energy reserves. Presumably, if there is insufficient rain to enable frogs to successfully breed then they feed and again go to ground waiting for more suitable conditions.

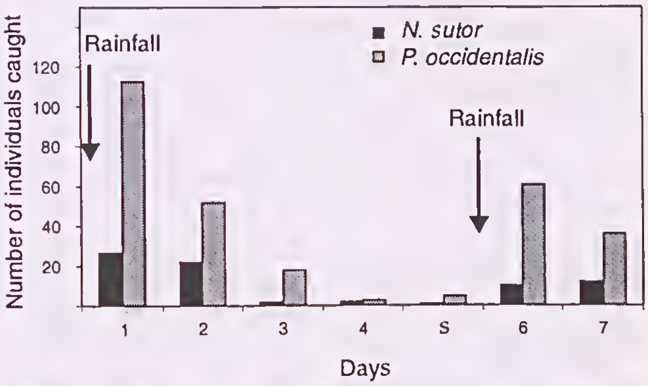

Figure 1. Number of *N. sutor* and *P. occidentalis* caught in pit-traps after rainfall.

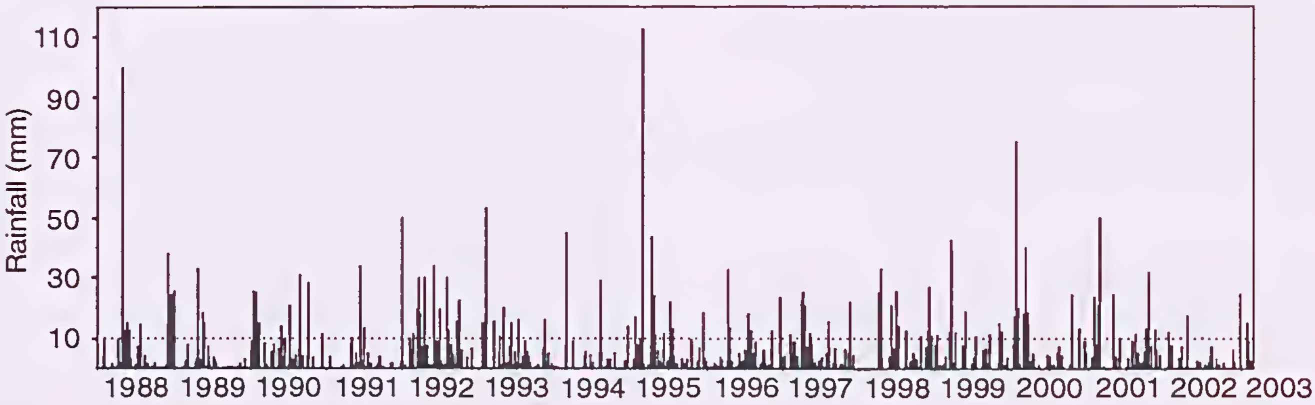

Figure 2. Rainfall measured on a daily cycle at the Placer Dome Asia Pacific Paddington gold mine, near Ora Banda. Dotted line shows the 10 mm level of rainfall.

Main (1968) reported that *N. sutor* breeds only in February and March, whereas *P. occidentalis* breeds between January and June. *Neobatrachus sutor* has a tadpole life of about 40 days and *P. occidentalis* has a larval development period of 30-40 days (Main 1968). The lack of large ponds likely to be present for four to five weeks in the undisturbed areas around Ora Banda precluded breeding by *N. sutor*.

We are convinced that most of the *N. sutor* that came to the surface after the rain on 27-28 January and 2-3 February did not breed but could have fed on the abundance of termites, and possibly other invertebrates. Diets of *N. sutor* and *P. occidentalis* are unknown; however, it is highly likely they eat a variety of invertebrates with a high proportion of termites, as Read (1999) reported *N. centralis* eating a wide variety of invertebrates but predominantly ants. Predavec & Dickman (1993) reported that diets of the arid-adapted sympatric *N. nichollsi*, *Cyclorana australis* and *N. centralis* in south-western Queensland varied but consisted mainly of Formicidae, Isoptera and Coleoptera.

Read (1999) reported that most *N. centralis* were caught on the surface after a minimum of 5 mm of rain. Our unpublished terrestrial fauna data for Ora Banda from September 2000 to June 2002 indicate that 5 mm of rain was insufficient to bring a substantial number of *N. sutor* to the surface (we only caught the occasional frog with 5 mm or less rain), but 4-6 mm of rain is sufficient for *P. occidentalis* to be surface active. *Pseudophryne occidentalis* can be found under rocks and leaf litter in moist locations when it has not rained for some time. They deposit their eggs on damp soil in tunnels and tadpoles emerge at an advanced stage of development when the tunnels flood with water (Main 1968; Tyler *et al*. 1994). A small amount of rain sufficient to create a few surface puddles and a damp environment appears to be sufficient for these frogs to become surface active. Cocooned and metabolically depressed *N. sutor* (Withers 1993, 1995) probably wait for more rain than *P. occidentalis* before they eat their cocoon, dig their way to the surface and become active. This species lays its eggs in ephemeral ponds during summer.

If *P. occidentalis* become surface active after 5 mm of rain, then using rainfall data since 1988 we calculate that they could have been active on an average of 17.5 occasions per year (Fig 2). This is an underestimate. Rainfall data are recorded for a 24 hour period and if rain occurred across a recording period this would have increased the number of opportunities for this species to be active. Similarly, we do not know if cumulative rainfall over a short period that provides a total in excess of this amount is also sufficient for this species to become surface active. If *N. sutor* require a minimum of 10 mm of rainfall to emerge then they could have been active on a minimum average of 9.3 occasions per year, but if they require 20 mm of rain this would have reduced the number of occasions they could have been active to 3.7 occasions per year. If *N. sutor* responds to cumulative rainfall over shorter periods then these will also be underestimates. Opportunities for *N. sutor* to successfully breed are obviously less than those to feed as they require temporary ponds that will last for at least 40 days (Main 1968) and to have formed during February and March. Because we are unsure of how much rain is required to create ponds that will last for at least 40 days during summer, we could not estimate the number of breeding opportunities over the last 15 years.

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Is the salinity of Lake Clifton (Yalgorup National Park) increasing?

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Abstract

Salinity of Lake Clifton, within Yalgorup National Park, Western Australia, varies annually in step with the annual change in water level. During the 1980s, salinity in the northernmost, permanent basin of the lake was hyposaline, varying between 8-32 g L^{-1}. By the late 1990s, however, recorded salinity values varied between 25-49 g L^{-1}. This brief communication serves to initiate discussion on whether salinity in the lake really is increasing. If the salinity is increasing, then the scientific values of this lake are threatened.

Keywords: Lake Clifton, salinity, Western Australia

Introduction

The limnologically-diverse lakes forming the Yalgorup National Park wetland (Fig 1) in south-western Western Australia constitute a natural laboratory of international scientific significance. The 10 km long reef of thrombolitic microbialites along the eastern shoreline of Lake Clifton (Moore *et al.* 1984) is a significant natural laboratory for investigating biogeochemical processes (Burne & Moore 1987; Moore 1987, 1990; Moore & Turner 1988; Moore & Burne 1994; Konishi *et al.* 2001). The lake is listed (jointly with lakes McLarty and Mealup and the Peel-Harvey Estuary) under the "Ramsar" Convention on wetlands as a Wetland of International Importance Especially as Waterfowl Habitat (Anon 1990).

Lake Clifton comprises essentially three basins; the northernmost is ~4.5 m deep and together with the middle basin is permanent; the southernmost basin dries out in summer. With no surface outflow and only occasional minor surface input (Davies & Lane 1996), the ~1 m annual fluctuation in water level of the lake is controlled by ground water and the balance between rainfall and evaporation.

Lake salinity

In March, 1972, Williams & Buckney (1976) recorded a salinity of 15.3 g L^{-1} in Lake Clifton. Moore (cited in Moore *et al.* 1984) recorded a salinity range of 17-30 g L^{-1} in 1979. In July 1983, after heavy rain, salinity of the lake near the aquifer outflow was 8.4 g L^{-1}. During the 1980s, Lake Clifton was hyposaline and the following salinity ranges were recorded; 17-26 g L^{-1} adjacent to transect A, 15-32 g L^{-1} adjacent to transect C, from two sites measured monthly in 1984 (Moore 1993). Values recorded monthly between May 1985, and July 1986, at the surface and near the bottom of the water column at three sites in

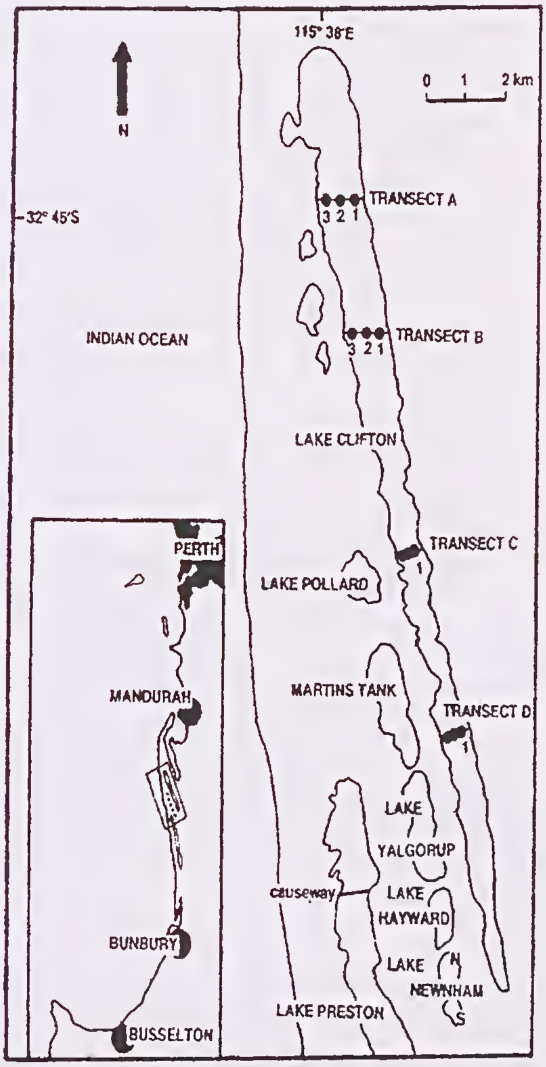

Figure 1. Lake Clifton and other lakes of the Yalgorup National Park. The inset shows the area of the main map, and the position of Lake Clifton relative to Bunbury and Mandurah. Sites C4 and F12 (in Moore 1993) are equivalent to transects A and C, respectively.

Table 1

Salinity values (g L^{-1}), Lake Clifton, 1985-86. Transects and sites are shown in Fig 1. Salinities in bold represent an average of differing top and bottom values.

	1985							1986					
	23 May	8 July	9-10 Aug	20 Sept	11-13 Oct	9-10 Nov	13-15 Dec	21-22 Jan	18-20 Feb	14-16 Mar	18-19 Apr	16-18 June	20-22 July
A1	32*	20	20	18	17	18	22	26	30	30	31.5	31	27
A2	32*	20	20	18	17	18	22	**25.5**	30	30	32	31	**27.5**
A3	31*	20	20	18	17	18	20	**25.5**	30	30	32	31	**28.5**
B1	26**		19	16	16	18	22	27	32	30	30	30	28
B2	27**		**20**	**17.5**	17	**17.5**	**21.5**	26.5	30	32	32	30.5	29
B3	27**		**20**	17	**15.5**	18	21	26	32	32	32	30	28
C1	30.5*	15	15	15	16	16	22	30	38	36	38	33	28
C2	30*	14	16	**14.5**	16	16	22	30	38	36	38	33	27
C3	32*	14	16	14	16	16	22	31				26	29
D1	26*	13	10	12	13	15	22	30	43	45	48	36	26
D2	26*	14	10	12	**13.5**	15	22	34	42	43	48	38	26
D3	26*	14	10	12	12	15	22	36	47			42	28

* 23 May 1985; ** 31 May 1985.

each of four transects (Table 1) showed ranges in the permanent, northern basin, transects A and B, of 17-32 and 15.5-32 g L^{-1} respectively. Salinity gradients reflect interactions between the position of freshwater inflow along the eastern margin, lake bathymetry and wind strength, which are sufficient to mix this lake vertically, but not horizontally. Salinity increased from north to south during the period of low water level (January-March 1986, Table 1), due to the increasing impact of evaporative concentration on successively shallower southern bodies of water. The gradient is reversed with high water level (in spring *e.g.* October 1985, Table 1); the northern basin (transect A) is most saline because of the higher salt load in the larger volume of water contained in the deeper basin. Successively lower salinities occurred along transects B-D during high water level, reflecting the greater impact of the freshwater input in shallower basins. Aquifer input was sufficient to generate an east-west salinity gradient, from 2 g L^{-1} immediately over the aquifer outflow, to 15 g L^{-1} at the edge of the rushes (*Juncus* sp; 23 August 1984, CM Burke & B Knott, unpublished data). Gilgies, *Cherax quinquecarinatus* (Gray), were active in this lens of fresher water at night.

A series of *ad hoc* salinity readings late in the 1990s suggest that salinity has increased since the 1980s. Values recorded at times of low water level have been; 44 g L^{-1} (adjacent to transect A; 17 May 1997, Konishi 1997); 49-34 g L^{-1} at site 2 (adjacent to transect C), and 45-25 g L^{-1} at site 3 (adjacent to transect D; Gartrell 1998); 48 g L^{-1} (adjacent to transect A, 24 April 1999). During the 1990s salinity values at times of high water level, too, have been higher than those noted in the 1980s; 25 g L^{-1} (both adjacent to transect A, 22 September 1999, and again on 5 September 2000).

Despite the limited evidence available, the data indicate that there has been an increase in salinity since the 1980s. The total annual rainfall at the two nearest meteorological stations, Bunbury and Mandurah, are plotted against water levels measured at Lake Clifton in September 1986 to 1999 (at the end of the rainy season) in Fig 2A. It is clear that there is a direct correlation between rainfall and water level in the lake. Measurements of salinity during the same period are shown in Fig 2B (J Lane, CALM, unpublished data). As expected, there is an inverse correlation between water level and salinity. However, if rainfall was the only driving factor in determining the lake's salinity, then increased rainfall in the late 1990s and the subsequent water level rise should have returned the salinity to the lower levels observed in the 1980s (during years of similar rainfall and water level). This trend has not been observed. An approximate estimation of the total salt content of the lake was calculated as the salinity multiplied by the total lake volume. Measurements of salinity were made in September when the lake was fully mixed, and lake volume was calculated as a function of water level based on bathymetry data supplied by the Water and Rivers Commission. These calculations indicate that although the mass of salt in Lake Clifton remained relatively constant from 1985 to 1992, it has since increased by 40% from 1993 to 2000 (Fig 2C). Since this calculation is independent of rainfall, this indicates a possible increase in proportion of brackish ground water to fresh ground water inflow into the lake. Clearly, further investigations are necessary to substantiate whether the observed increases in salinity of Lake Clifton are permanent, and if so what are the cause(s).

Consequences

If the salinity of Lake Clifton is increasing and continues to do so, then changes in the pattern of microbialite growth, reduction in faunal diversity within the lake, and change in usage by waterbirds, are inevitable consequences unless the cause(s) are identified and corrected. Even if the salinity is increasing, any ecological perturbations already in train may not yet be irreversible given immediate remedial action. The limnology of Lake Hayward altered substantially during the dry summer of 1987/1988, but subsequently returned to its pre-drought pattern, probably through internal homeostatic mechanisms (Burke & Knott 1997). With a permanent change to hypersalinity, the international scientific significance of the lake may well be lost. It must

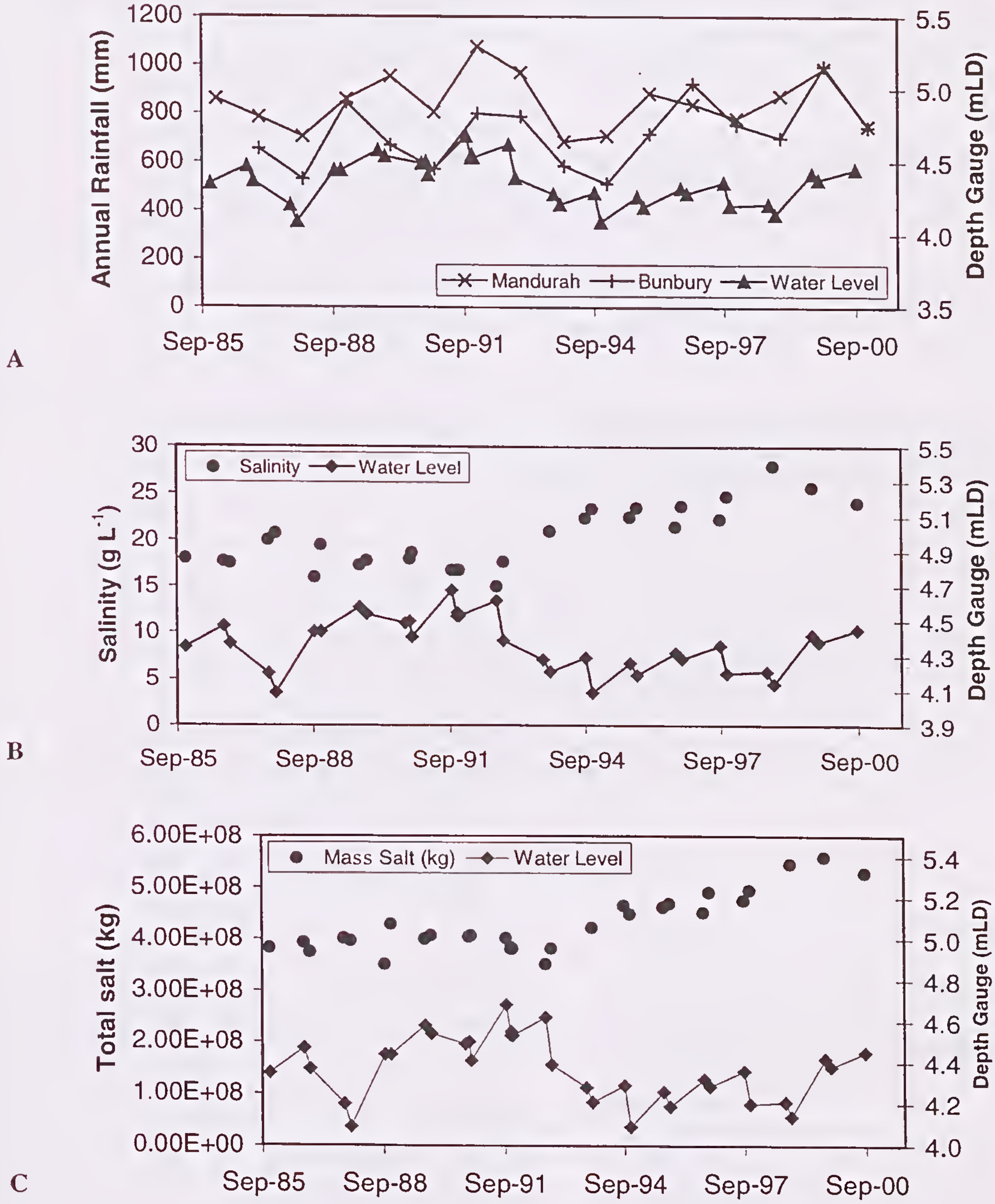

Figure 2. A comparison of changes in annual rainfall, water level and salinity of Lake Clifton 1985 to 1999. A: Rainfall and water level data. B: Salinity and water level data. C: Total salt and water level data. mLD = mean lake data, equivalent to Australian height datum + 4.035 m. Rainfall data from the Commonwealth of Australia Bureau of Meteorology; water level and salinity measurements from the Western Australian Department of Conservation and Land Management.

also be acknowledged that concerted action by the government departments responsible for managing the environment may be required to prevent them presiding over the irreversible loss of a major scientific laboratory of international standing.

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Conservation status of *Goodenia* (Goodeniaceae) in Western Australia, including a review of threatened, rare and poorly known species

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Abstract

A comprehensive assessment of the current conservation status of *Goodenia* in Western Australia was based on information from herbarium labels at the Western Australian Herbarium (PERTH), Western Australian Department of Conservation & Land Management (CALM) filed information, original observations by the authors, the Flora of Australia volume 35, and personal communication with other botanists. Species diversity and conservation-listed taxa are assessed according to the Interim Biogeographic Regions of Australia for Western Australia. Phytogeography, biology, current conservation listings, threatening processes, apparent causes of rarity, and management and research recommendations are discussed. Many *Goodenia* are highly responsive to disturbance and prefer water-gaining sites, the margins of watercourses, or depressions. Highest diversity and conservation-listed taxa occur in the sand plain heaths of the South-West Botanical province. Recommended management procedures include a careful fire regime after research into the reproductive biology of a species, reserve design to include habitat preferences, floristic surveys of nearly all the conservation-listed, emergency actions to address threats in the South-West Botanical Province, and *ex situ* conservation measures once the true conservation status of a species is determined. *Goodenia* in Western Australia is unsatisfactorily known, with many requiring further surveying and monitoring, and over 40% of taxa listed on CALM Priority flora lists. Research into the biological, taxonomic and genetic resources of *Goodenia* is required for their effective and successful conservation.

Keywords: *Goodenia*, Goodeniaceae, Western Australia, diversity, conservation, management

Introduction

The Goodeniaceae is an indicative Australian angiosperm plant family that is "strongly significant in the Australian flora" and is well represented in the Western Australian flora (Marchant 1973; Elliot & Jones 1986). The Goodeniaceae are commonly encountered in the heathlands and shrublands in the South-West Botanical province of Western Australia (George *et al.* 1979). There are 11 genera in the family, with *Goodenia* Smith the largest genus (Carolin 1992) of over 190 species, with about 120 in Western Australia (Paczkowska & Chapman 2000; LWS, unpublished data). All but three species of *Goodenia* are endemic to Australia (Carolin 1992; Elliot & Jones 1986).

Goodenia species occur in a wide variety of temperate habitats (Elliot & Jones 1986) usually around the edges of lakes and watercourses in the arid interior (Table 1). Most *Goodenia* species are perennial sub-shrubs and forbs or annual herbs, although species such as *G. grandiflora* and *G. scapigera* are shrubs. Species are usually perennial and resprouters, responding well after disturbance (Table 2), but others are annual reseeders.

We examined specimens for taxonomic studies in Western Australian *Goodenia* (Cranfield & Sage 1997; Sage 1998; Sage & Pigott 1998; Sage 2000, 2001). We found that an overall assessment of the conservation status was required on this little studied genus. Of an estimated 120 Western Australian species of *Goodenia*, 22 were listed by the Western Australian Department of Conservation and Land Management (CALM) as threatened or poorly known (CALM filed information). This study added another 25, to total over 40% of the genus for the state.

This paper surveys the genus *Goodenia* in Western Australia for apparent rarity, potential threats and appropriate management and research recommendations.

Methods

Data on species abundance were obtained from field observations, from CALM filed information (unpublished data), the Flora of Australia volume 35 (Goodeniaceae), herbarium specimens, herbarium label information at the Western Australian Herbarium (PERTH), and personal communication with other botanists. Nomenclature of Western Australian species follows Carolin (1992) and recently published work (Sage 1998, 2000, 2001). Undescribed, distinctive species are included in this study.

All other names follow WACENSUS (Western

Table 1

Water-associated habitat observations of Western Australian conservation-listed *Goodenia* (taken from label information for collections at the Western Australian Herbarium, Perth). Conservation status (CALM) as of December 2001; see Table 3 for priority codes.

Species	Status	Comment	Voucher
Goodenia byrnesii	P1	"In sand at edge of creek"	H F Broadbent 624
Goodenia crenata	P3	"Margins to billabong"	D Dureau 118
Goodenia durackiana	P1	"On black cracking clay soil"	M Lazarides 6743
Goodenia filiformis	P3	"Sandy swamp"	E J Croxford 1359
Goodenia gloeophylla	P2	"Along small creekline"	D E Symon 7125
Goodenia inundata	P2	"Rocks in river.."	G J Keighery 9089
Goodenia kakadu	P3	"On damp mud at edge of swamp"	I Cowie 4378
Goodenia lyrata	P1	"...drainage tract in hardpan plain"	A L Payne PRP 1349
Goodenia neogoodenia	P4	"Damp flat at edge of claypan"	S Patrick *et al.* 41
Goodenia nuda	P3	"Bare river sand in dry scoured river bed"	K McCreery ecol 96
Goodenia omearana	P1	"Swamp on major river floodplain"	A A Mitchell PRP 727
Goodenia purpurascens	P3	"Bed of river"	A S Mitchell 756
Goodenia schwerinensis	P3	"...along creek line"	A S George 8160
Goodenia stenophylla	P4	"In creek bed"	A S George 7191
Goodenia strangfordii	P1	"On damp clay flat"	J H Willis sn
Goodenia virgata	P2	"...drainage line"	A R Annels ARA 12 A
Goodenia sp Scaddan (CD Turley 41 VM/1099)	P1	"...close to lake edge"	C D Turley 41 VM/1099

Table 2

Disturbance observations for Western Australian conservation-listed *Goodenia* taxa (taken from label information from collections at the Western Australian Herbarium, Perth). Conservation status (CALM) as of December 2001; see Table 3 for priority codes.

Species	Status	Comment	Voucher
Goodenia arthrotricha	P2	"In scrub burnt previous summer"	V Mann & A S George 202
Goodenia brachypoda	P1	"Burnt area"	N F Norris 863
Goodenia gibbosa	P1	"Growing in recently burnt area"	B & B Backhouse W 206
Goodenia laevis	P3	"Area ? recently slashed..."	C D Turley 10/1295
Goodenia modesta	P3	"Recent fire..."	C P Campbell 378
Goodenia perryi	P3	"...restricted to disturbed areas.."	M Hislop 1848
Goodenia qudrilocularis	P2	"...spread by roadside disturbance"	C D Turley 13/497
Goodenia schwerinensis	P3	"In burnt patch..."	D J Edinger *et al.* DJE2183A
Goodenia sericostachya	P3	"...disturbed road verge"	A S George 16407
Goodenia trichophylla	P3	"Burnt 18 months previously"	M Officer B 13
Goodenia sp South Coast (AR Annels ARA1846)	P3	"Gravel pit"	E J Croxford 4304

Australian Herbarium database of vascular plant names for Western Australia, December 2001), Green (1985) and Albrecht (2002). All data for maps were sourced from WAHERB (PERTH) database of specimen collections and mapped using ArcView 3.1 (ESRI). See Table 3 for an explanation of the CALM Priority listing codes.

Results

Biology and ecological preference

As discussed above, most *Goodenia* species have habitat preferences for the margins of water gaining sites, depressions and watercourses (Table 1). This is true for the South-West and Northern Botanical Provinces, although most evident in the Eremaean Botanical Province where *Goodenia* species are either annuals or annually regenerate from a rootstock. Table 1 gives conservation-listed *Goodenia* species lodged with the Western Australian Herbarium collected from such habitats. "The presence and relative abundance of plants (*G. halophila* and *G. cylindrocarpa*, from central Australia) at a particular site each year appears to be highly dependant on the amount of rainfall" (Albrecht 2002).

Many *Goodenia* taxa are highly responsive to fire (re-sprouters or fire/ disturbance opportunists). Table 2 lists *Goodenia* species lodged with the Western Australian Herbarium collected from recently disturbed habitats that indicate this functional trait. *G. sericostachya*, a poorly known species (CALM Priority Three), shows this response. Observed to be in abundance the year after a fire, population numbers rapidly fell in the following seasons to total absence after seven years (CALM filed information). Similar responses have also been observed for the related genera *Scaevola* and *Lechenaultia* (LWS, unpublished data; GJ Howell, NSW Agriculture, personal communication). Populations of *Lechenaultia striata* in the Little Sandy Desert were seen in the thousands the year

Table 3

CALM categories of Priority Flora according to the degree of perceived threat (after Atkins 1998).

Category	
R: Declared Rare Flora Extant taxa (= Threatened Flora = Endangered + Vulnerable)	Taxa that have been adequately searched for, and are deemed to be in the wild either rare, in danger of extinction, or otherwise in need of special protection
X: Declared Rare Flora Presumed Extinct taxa	Taxa that have not been collected or otherwise verified over the past 50 years *etc*
1: Priority One Poorly Known Taxa	Taxa that are known from one or a few (generally < 5) populations which are under threat
2: Priority Two Poorly Known Taxa	Taxa that are known from one or a few (generally < 5) populations, at least some of which are not believed to be under immediate threat (*i.e.* not currently endangered)
3: Priority Three Poorly Known Taxa	Taxa that are known from several populations, at least some of which are not believed to be under immediate threat (*i.e.* not currently endangered)
4: Priority Four Rare Taxa	Taxa that are considered to have been adequately surveyed and which, while being rare (in Australia), are not currently threatened by any identifiable factors

after fire and adequate rain only to decline in the following years (S van Leeuwen, CALM, personal communication).

Nearly 80% of perennial species on granite habitats at Chiddarcooping Hill Nature Reserve were obligate seeders likely to be killed by fire (Hopper 2000). This is relevant to the CALM Priority listed taxa on granite outcrop habitats such as *Goodenia drummondii* subsp *megaphylla* (CALM Priority Three) and *G. scapigera* subsp *graniticola* (CALM Priority Two).

Goodenia species can generally be classed in terms of life history strategy as annuals (*e.g. Goodenia berringbinensis*), resprouters (*e.g. Goodenia stellata*) and disturbance opportunists (*e.g. Goodenia decursiva*). Similar numbers of annual and perennial species occur in the threatened or poorly known groups as in the abundant categories.

Phytogeography

The total number of *Goodenia* taxa recorded from material at the Western Australian Herbarium (PERTH) for the Interim Biogeographical Regions of Australia or IBRA (Thackway & Cresswell 1995) are shown in Fig 1. The highly species-rich South-West Botanical Province is reflected in *Goodenia* with over 40 taxa occurring in the region (Carolin 1992). Highest diversity occurs on the sand plain heaths of the Avon Wheatbelt, Mallee and Esperance Plains IBRA (or bioregion) rather than the wetter forest areas of the lower south-west or the arid interior. This is consistent with that observed for the general floristic pattern of the province (Hopper 1979). The nearby Murchison IBRA of the Eremaean Botanical Province shows diversity equal to that of these regions. The intervening Yalgoo and Coolgardie bioregions have fewer species (11-15 and 26-30 taxa respectively). This may indicate a low level of collector effort in these regions, although the Murchison IBRA is significantly larger in area.

Less diversity is found in the species-rich Geraldton Sandplains IBRA (16-20 taxa). This compares with *Darwinia* and *Stylidium*, which also have less diversity in the Geraldton Sandplains compared with higher levels in regions such as the Avon Wheatbelt (Paczkowska & Chapman 2000).

The highest diversity in the Eremaean province occurs in the Murchison IBRA (31-35 taxa). The Pilbara bioregion (26-30 taxa) has the next highest number of species, with the central and north-west bioregions of Carnarvon, Gascoyne and the Little Sandy Desert closely following (21-25 taxa). This may be due to the diversity of habitat in these regions and a factor of higher collector effort in these regions compared to the rest of the province. The level of diversity declines in the east of the province to 0-5 taxa for the Nullarbor Hampton bioregions in the extreme south-east, though this is only for the Western Australian component of these bioregions.

In the Northern Botanical province diversity is highest in the Northern Kimberley bioregion, gradually decreasing to the south-east. Only the Western Australian components of the Tanami, Victoria Bonaparte and Ord-Victoria Plains were taken into account.

Goodenia in Western Australia is 60% endemic (Hopper *et al.* 1996, based on Carolin 1992). This is less than the average of 75% endemism for Western Australia and lower than other herbaceous genera such as *Dampiera* (91%), *Scaevola* (95%) and *Drosera* (80%). The number of *Goodenia* in the Eremaean and Northern Botanical Province whose range extends into the Northern Territory and South Australia may account for this lower level of endemism.

Threatened, rare or poorly known

Of 22 *Goodenia* species listed by CALM as Priority flora prior to this study, only one is threatened and none are presumed extinct (K Atkins, CALM, personal communication). As a result of this work a further 25 taxa were added to the CALM's Priority listings, resulting in over 40% of the genus in the state being conservation-listed. The low number of *Goodenia* species

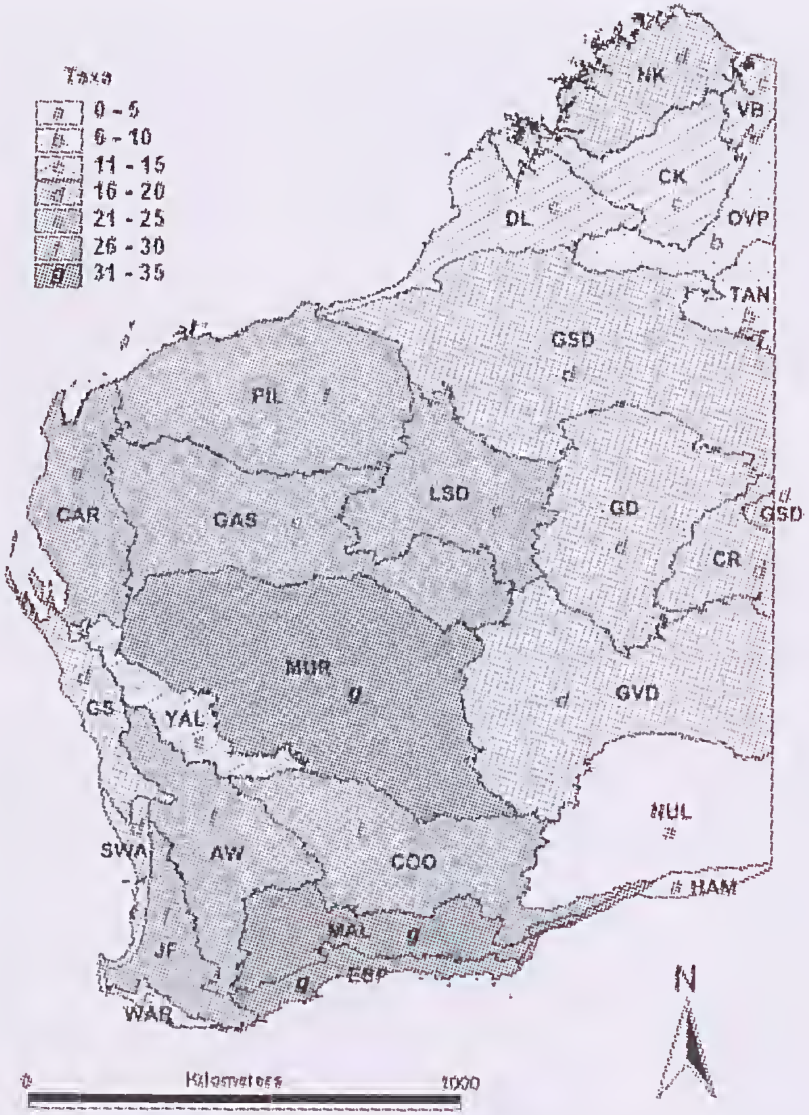

Figure 1. Total number of *Goodenia* taxa recorded for each IBRA according to PERTH (Southwest Botanical Province: AW= Avon Wheatbelt; ESP= Esperance Sandplains; GS= Geraldton Sandplains; JF= Jarrah Forest; MAL= Mallee; SWA= Swan Coastal Plain; WAR= Warren. Eremaean Botanical Province: CAR= Carnarvon; CR= Central Ranges; COO= Coolgardie; HAM= Hampton; GAS= Gascoyne; GD= Gibson Desert; GSD= Great Sandy Desert; GVD= Great Victoria Desert; MUR= Murchison; NUL= Nullabor; LSD= Little Sandy Desert; PIL= Pilbara; YAL= Yalgoo. Northern Botanical Province: CK= Central Kimberley; DL= Dampierland; NK= Northern Kimberley; OVP= Ord- Victoria Plain; TAN= Tanami).

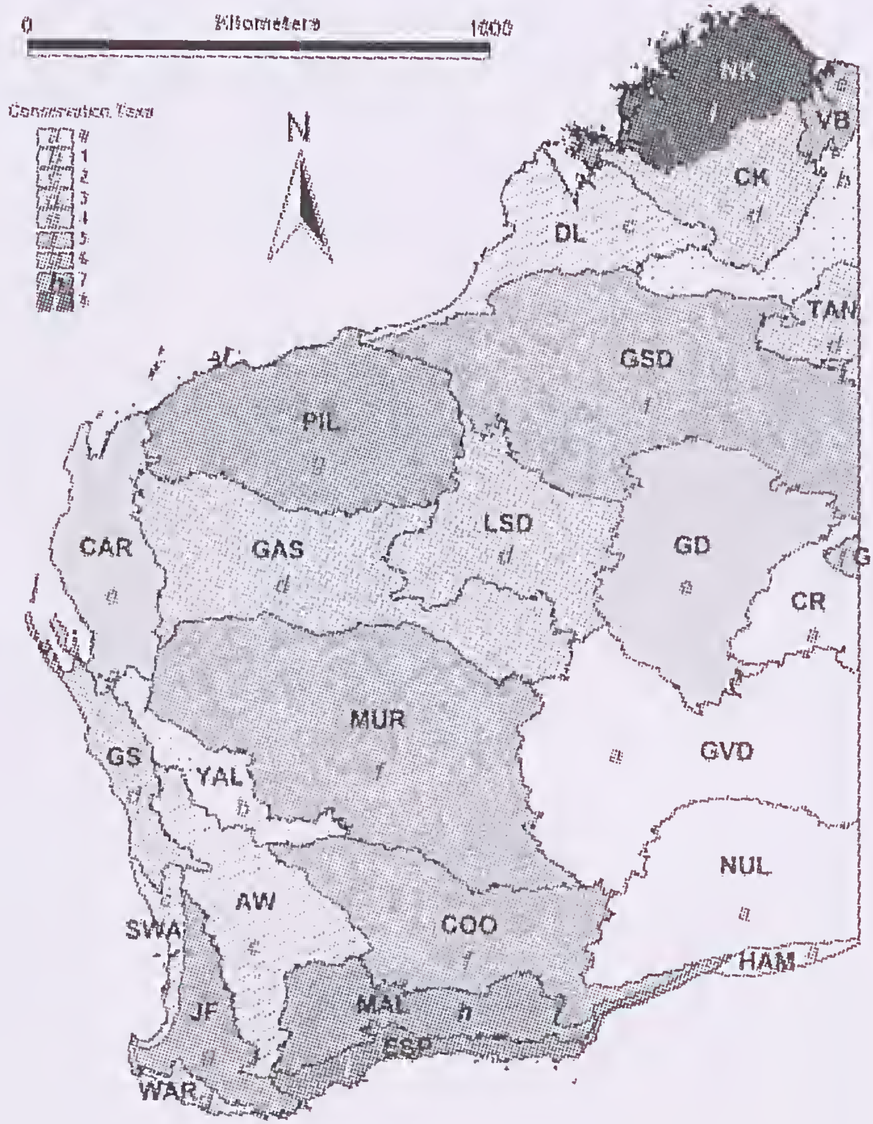

Figure 2. Total number of *Goodenia* conservation-listed taxa for each IBRA in Western Australia, as of December 2001.

currently listed as threatened may reflect the relatively recent publication of the Flora of Australia in 1992 and the paucity of previous work in Western Australia. A taxon cannot be upgraded to threatened unless it has been thoroughly searched for in the wild by botanists in the past five years and been shown to be rare or under some threat of extinction (Brown *et al.* 1998).

The number of threatened, rare or poorly known *Goodenia* species are shown for the IBRA for Western Australia in Fig. 2. The highest numbers occur in the species rich South-West Botanical Province, specifically the Esperance Plains IBRA, the area of highest diversity, survey effort, and habitat destruction and disturbance. The Northern Kimberley and the Esperance Sandplains IBRA each have eight species of conservation listed taxa. This high level of conservation-listed taxa in the Northern Kimberley may be due to the bioregion having the highest diversity of the Northern province and being very poorly collected. Prior to this study, very few conservation taxa were known to occur in the Eremaean or Northern botanical province, though the majority of the newly recommended taxa occur there.

An estimated 45% of populations of threatened or poorly known *Goodenia* species occur on the conservation estate *i.e.* reserves, national parks and state forest and local government reserves (K Atkins, CALM, unpublished data). This compares favourably with 37.9% for the all of the threatened species in the State (K Atkins, CALM, unpublished data).

The following 25 taxa were added to the CALM Codes for Priority Flora listings (see Appendix 1 for a detailed account of each taxon) as a result of this study; *Goodenia berringbinensis, G. brachypoda, G. byrnesii, G. crenata, G. gibbosa, G. gloeophylla, G. grandiflora, G. hartiana, G. heatheriana, G. janamba, G. kakadu, G. lunata, G. modesta, G. omearana, G. pascua, G. salmoniana, G. purpurascens, G. schwerinensis, G. strangfordii, G. suffrutescens, G.* sp Lake King (*M Gustafsson et K Bremer* 132) , *G.* sp Scaddan (*C D Turley* 41VM/1099), *G.* sp South Coast (*A R Annels* ARA1846), *G. virgata* and *G. varia.*

Discussion

Threatening processes

Threatening processes affecting Western Australian *Goodenia* were observed by the authors and other botanists. They can often be inferred from the habitats the species occur in, the life history strategy and general threats to other species as discussed in Brown *et al.* (1998). Critically small remnants are directly threatened by degradation and destruction (Coates & Atkins 2001). Other threats are introduced weeds, *Phytophthora* root rot disease, and feral and agricultural animal grazing. All specifically relate to the highly altered and fragmented *Goodenia*-'rich' Kwongan sand plain heaths of the South-West Botanical Province, and except for *Phytophthora* are relevant to the Eremean and Northern Botanical Provinces. Overall these processes vary between IBRA and the broader Botanical Provinces.

Rising salinity and water tables is a significant problem to the flora of the South-West Botanical Province (Brown *et al.* 1998) and threatens species such as *Goodenia integerrima* (currently listed as threatened by CALM) and *G.* sp Lake King (*M Gustafsson et K Bremer* 132). Both taxa occur in halophytic vegetation on the edge of a few salt lakes in the Avon Wheatbelt IBRA (and are therefore saline tolerant at some level).

Phytophthora cinnamomi root rot disease is a significant threat to the families Proteaceae, Epacridaceae, Papilionaceae and Myrtaceae of the South-West Botanical Province (Brown *et al.* 1998). Goodeniaceae in general are affected as the family is the sixth highest vascular plant family affected by plant pathogens, including *Phytophthora cinnamomi*, rusts and other fungal infections (Shearer 1994). The related genera *Dampiera* and *Scaevola* (Goodeniaceae) are susceptible to *Phytophthora* species infection (Malajckuk & Glenn 1981; McDougall *et al.* 2001). Thus species of threatened or poorly known *Goodenia* occurring within the higher rainfall zones of the South-West Botanical Province should be treated as potentially susceptible to *Phytophthora* root rot disease.

Invasive weeds are a major threat in the highly fragmented Avon Wheatbelt IBRA. Agriculture has altered this bioregion from a vast mosaic of perennial vegetation associations to only small remaining fragments of native vegetation (Hobbs 1998; Scanlan *et al.* 1992). A survey of the relatively undisturbed Yilliminning Rock Reserve (east of Narrogin in the central Avon Wheatbelt IBRA) found 8% of flora to be introduced weeds (Pigott & Sage 1997). Another survey found 10% of plant species in Jingaring Nature Reserve to be introduced weeds (Obbens *et al.* 2001). These percentages are consistent with relatively undisturbed remnants, while highly disturbed remnants contain much higher percentages. Generally weeds are difficult to remove once introduced, and prevent perennial species regenerating (Hobbs & Atkins 1991). This threat is highly relevant to the *Goodenia*-"rich" Avon Wheatbelt IBRA and should be addressed in any management regimes for threatened or poorly known *Goodenia*.

For the Eremaean and Northern Botanical Provinces the main threatening process are feral and agricultural herbivores that degrade the margins of water bodies, a major habitat of *Goodenia* species. Pickard (1993) states that semi-arid ecosystems, such as the margins of water bodies, are under threat from current land use practices involving domestic and feral herbivores as well as feral carnivores. Mining activities may also be a threat, especially in the Pilbara where species have small distributions or restricted habitats.

Apparent causes of rarity

Loss of suitable habitat, through natural or anthropogenic processes, for those species that are habitat dependent and occur in regions of the greatest habitat destruction (such as the South-West Botanical Province) may be a cause of rarity in certain *Goodenia* species. *Goodenia katabudjar* is an example of habitat limitation mostly through anthropogenic habitat destruction (Cranfield & Sage 1997). This species is restricted to upland Jarrah-Wandoo woodland intergrade on the central border of the Jarrah Forest and Avon Wheatbelt IBRA, which has been cleared over most of its known range. Recently discovered and described, this species is known from only three populations and is under immediate threat from mining activities (Cranfield

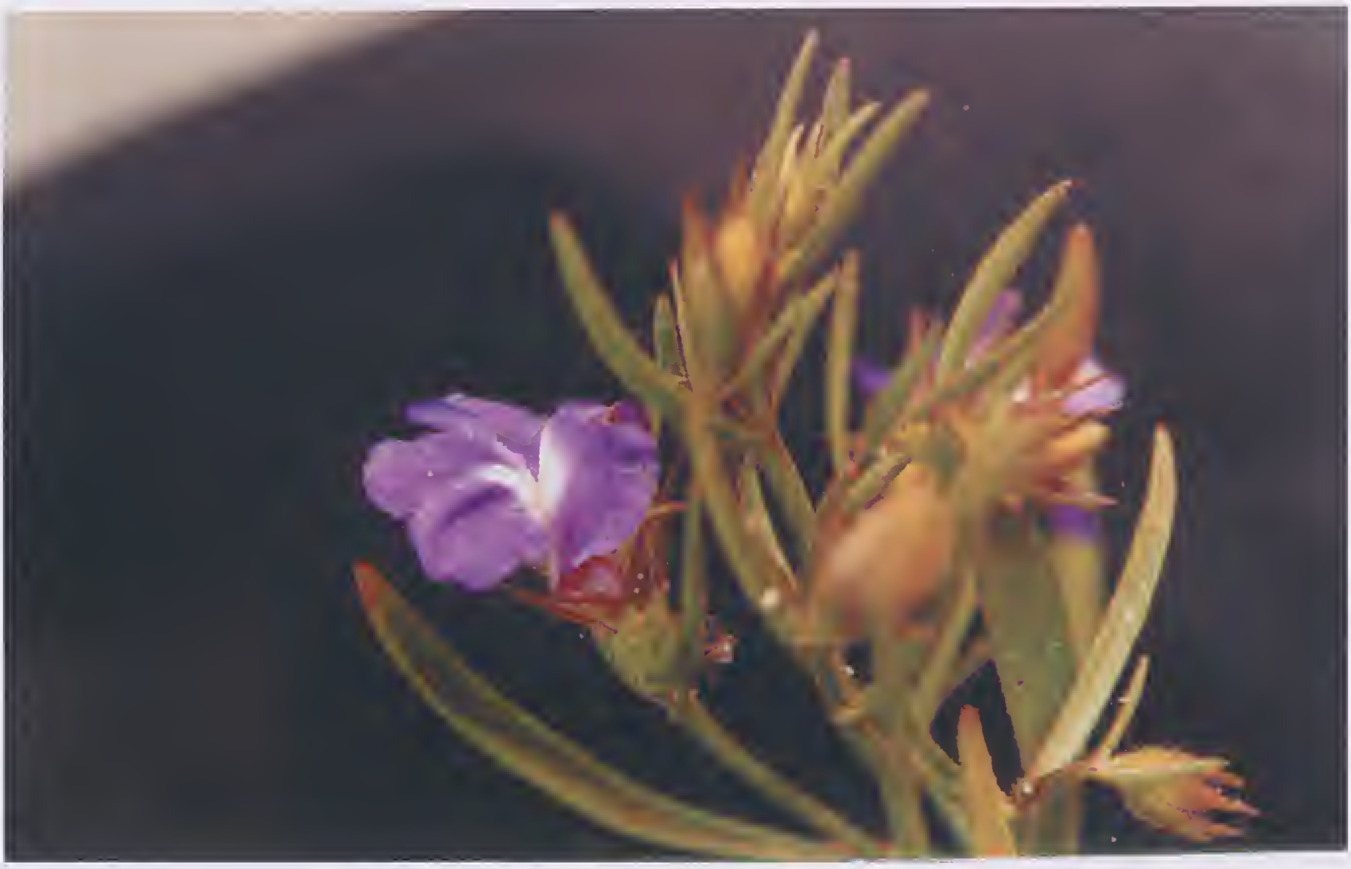

Figure 3. *Goodenia arthrotricha* Benth (photograph by H Bowler, used with permission).

& Sage 1997). Urgent field surveys are required to determine the true conservation status of this species.

Difficulty in identification can hinder knowledge of a species and survey work. *Goodenia* can be relatively difficult to identify correctly as some species are polymorphic and diagnostic characters can be hard to recognize. Taxonomic bias can contribute to this. Some of the perennial species tend to die off in summer, and without adequate flowering material identification may be impossible, or the species may be totally missed by collectors (*e.g. Goodenia arthrotricha*, is often confused with *Scaevola calliptera*; Fig 3).

Low collector effort (*i.e.* few herbarium specimens collected and lodged for a given area) can create an apparent rarity of a species particularly when herbarium specimens are the sole source of population data (Fig 4). An example of this is *Goodenia drummondii* sp *megaphylla*, a new subspecies only recently described from the Jarrah Forest IBRA near the Perth metropolitan area (Sage 1998). This taxon was listed as a Priority Three species with only a few known populations. Recent collector effort in the area has turned up a further fifteen populations, all in state forest. Thus we recommend the taxon for removal from the Priority list.

Fig 4 illustrates the total collector effort for *Goodenia* lodged at the Western Australian Herbarium. As expected, the highest concentration of collector effort is in the south-west of the state, becoming more restricted to major roads towards the interior. Hence some poorly known species, from poorly collected areas, might more be a factor of collector effort than actual rarity.

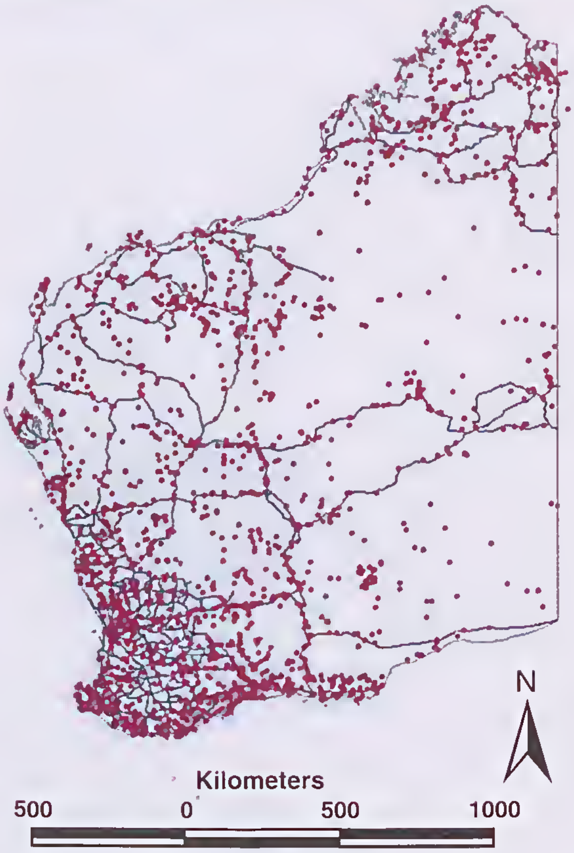

Figure 4. Total *Goodenia* collector effort for Western Australia (WA Herbarium; PERTH) as of September 1999; major roads are shown.

Collections from the South-West Botanical Province may give a more accurate picture of conservation status than collections from either the Eremaean or Northern Botanical Provinces (Fig 4). An assessment scale in relation to collector effort for each Botanical Province may help determine the conservation status for respective taxa. However even in the 'better' collected South-West Botanical Province there are large collecting "gaps" due to various factors such as accessibility (P Gioia, CALM, personal communication). This may be taken into account when making a conservation assessment of a species from the Eremaean or Northern Botanical Provinces, though difficult to assess. The CALM Priority rankings are used to indicate areas where further surveying is currently required for poorly known species and this is relevant for a species regardless of its region (or that region's collector effort). In the Eremaean and Northern Botanical Provinces *Goodenia* species are more likely to be associated with water bodies but roads (concentrations of collector effort) are built to follow ridges and avoid drainage lines (Burgman & Lindenmayer 1998).

Management and research considerations

A clear understanding of plant taxonomic and genetic resources is required for effective and successful biological conservation (Hopper 1994). This is highly relevant to *Goodenia* and the Goodeniaceae in general, which are currently poorly known in both areas. This may be a consequence of resources and interest being directed towards previously listed conservation taxa as currently only *Goodenia integerima* is legislatively protected as threatened or declared rare flora. This work aims to direct attention to species of *Goodenia* and Goodeniaceae recommended for conservation listing. We are working towards delineating the taxa in *Goodenia* that require further conservation efforts (Hopper 1994). Determining (genetic) conservation units in threatened taxa that allows a delineation of suitable units for conservation also provides the appropriate geographical scale for management (Coates 2000). This is relevant to the highly fragmented *Goodenia*-'rich' South-West Botanical Province.

We recommend the following procedures for managing threatened, rare and poorly known *Goodenia*;

1. **Fire Regimes.** Fire regimes for reserves that contain threatened, rare or poorly known *Goodenia* should take into account the fire response of the individual species involved and the habitat type. Research into the longevity of the seed soil bank and the reproductive biology of species is a priority. Non-invasive practices such as smoke-induced seed germination (Roche *et al.* 1998) should be considered in any managment program. Most *Goodenia* species respond favourably after a fire event, often demonstrating the true abundance of a species (Table 2). Some species of *Scaevola* may "disappear" if fire is excluded from a management regime (GJ Howell, NSW Agriculture, personal communication) and this may be the case for *Goodenia* as well.
2. **Reserve Design.** Reserve design should take into account the habitat preference of *Goodenia* species for the margins of water bodies and water gaining sites. *Goodenia* are often found associated with water features (temporary lakes and watercourses) in central Australia, although this is not indicative of an aquatic phase (Table 1). Their habitat is often not covered by arbitrary reserve boundaries or may be affected by upstream water flow (salinity, silt or nutrients). Reserve design should also ideally support pollinators. Population management should include the genetic resources of species and plant numbers as well as the availability and abundance of pollinators (Coates & Atkins 2001).
3. **Flora Surveys.** Urgent surveys are required for nearly all conservation-listed *Goodenia* taxa in Western Australia. Only *G. neogoodenia*, *G. stellata* and *G. integerrima* have been adequately searched for in the wild. Survey efforts in the Eremaean and Northern Botanical Provinces should be directed to those conservation-listed taxa that are threatened by mining unless the taxon is highly restricted or otherwise requires immediate attention (*e.g. Goodenia salmoniana*, which is known only from the holotype collection, made in 1889). Collected material should be identified by specialist botanists, as some Western Australia *Goodenia* are problematic (*e.g. Goodenia* aff *pascua*, currently being examined by LWS).
4. **Threats.** Measures to protect conservation-listed *Goodenia* in the South-West botanical province, specifically the Avon Wheatbelt IBRA, are essential to the future survival of species such as *G. intergerrima* and *Goodenia* sp Lake King (*M Gustafsson et K Bremer* 132) which are under direct threat from rising salinity and hydrological changes.
5. ***Ex situ* conservation.** Once a better understanding of the true conservation status of many *Goodenia* conservation taxa is gained, cryogenic storage and long term seed banking should be undertaken for those species requiring it.

Conclusion

Goodenia in Western Australia is unsatisfactorily known and requires further surveying and monitoring, and biological research. Many taxa have never been surveyed or are known from a few historical collections or only a holotype collection and little is known of their biology. Over 40% of Western Australian *Goodenia* species are now on CALM Conservation Codes for Western Australian Flora Priority lists. Many species may prove to be more common than currently thought due to factors such as poor collector effort, taxonomic bias and difficulty in identification. Life history strategy may affect the abundance of *Goodenia* species at any given point in time. Relatively similar numbers of annuals and perennials occur among poorly known and abundant species. Though quite well conserved on the conservation estate in the South-West Botanical Province, *Goodenia* species are under direct threats from land clearing, rising salinity, invasive weeds and habitat degradation, including the margins of water points in the Eremaean and Northern Botanical Provinces, a major *Goodenia* habitat in these regions. We would encourage professional and amateur botanists with the relevant licenses to lodge good material of *Goodenia* species with accurate site and plant details with the Western

Australian Herbarium (PERTH), as this can contribute significantly to the knowledge of our flora.

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Appendix 1

Conservation-listed *Goodenia* from Western Australia. Data taken from CALM filed information and Western Herbarium (PERTH) label information, as of December 2001.

Taxa	Status * (CALM; ROTAP)	Number of populations (total; in conservation reserves)	WA Distribution (IBRA)	Number of plants (estimated)	Main threats	Closest relative	Notes
1. *Goodenia anfracta*	P1; 3K	3; 0	GSD	?	?	*G. fascicularis*	Surveys required; photograph of holotype for PERTH; very poorly known in WA.
2. *Goodenia arthrotricha*	P1; 2K	*ca* 4; 1	SWA	< 50	urban clearing	-	Urgent surveys required; populations of scattered individuals.
3. *Goodenia berringbinensis*	P1; 3K	4; 0	CAR, MUR, GAS	> 1000	water point degradation	-	Probably more common than is apparent; requires surveys.
4. *Goodenia brachypoda*	P2; 2K	5; 0	VB	?	unknown	*G. sepalosa*	Restricted range; very poorly known.
5. *Goodenia byrnesii*	P1; 1K	1; 0	DL	?	water point degradation	*G. sepalosa*	Extended range across northern Australia, although poorly known in WA.
6. *Goodenia crenata*	P3; 3K	5; 0	TAN, OVP, CK	> 500	?	*G. hirsuta*	Probably more common than is apparent.
7. *Goodenia drummondii* subsp *megaphylla*	P3; 3C-	15; *ca* 2	JF, AW	> 500	?	*G. helmsii*	Not currently under immediate threat with some populations on reserves.
8. *Goodenia durackiana*	P1; 2K	2; ?	CK, VB	?	?	*G. leiosperma*	Surveys required.
9. *Goodenia filiformis*	P3; 2KC-	*ca* 6; 1	WA, ESP	< 300	land clearing	*G. pulchella*	Confusion with *G. pulchella*.
10. *Goodenia gibbosa*	P1; -	*ca* 3; 0	CR	?	?	*G. pinnatifida*	Common and widely distributed in the NT; surveys required.
11. *Goodenia gloeophylla*	P2; -	*ca* 2; 0	NK	< 100	?	*G. purpurascens*	Widely distributed across NT.
12. *Goodenia grandiflora*	P1; -	1; 0	CR	< 50	?	*G. kingiana*	A variable species common across eastern central Australia, although very poorly known in WA.
13. *Goodenia hartiana*	P2; 2K	2; 0	GSD, LSD	< 100	mining activities	*G. azurea*	May prove to more common than apparent, due to visual similarity to *G. azurea*.
14. *Goodenia heatheriana*	P1; 2K	*ca* 3; 0	AW, COO	< 100	mining activities	*G. pinnatifida*	Urgent surveys required; previously unsuccessfully searched for.
15. *Goodenia hirsuta*	P1; -	?	?	?	?	*G. cycloptera*	No collections located at PERTH; distribution unknown.
16. *Goodenia integerrima*	Endangered; 2ECiT	2; 2	AW	< 50	salinity, hydrological change	-	Known from only a handful of plants in 2 populations.
17. *Goodenia jenamba*	P1; -	3; 0	DL, NK, VB	?	?	-	May prove to be more common than apparent.
18. *Goodenia kakadu*	P3; -	5; ?	NK	?	?	*G. pumilo*	Found in NT and may prove to be more common than is apparent.
19. *Goodenia katabudjar*	P2; 2K	3; 0	JF	< 150	mining activities	*G. leptoclada*	Urgent surveys required as is under threat from mining activities.
20. *Goodenia laevis* subsp *laevis*	P3; 3K	6; 0	COO, ESP, MAL	< 600	?	*G. laevis* ssp *humifusa*	Surveys required.
21. *Goodenia lunata*	P1; -	1; 0	CK	?	?	*G. fascicularis*	Common throughout inland eastern Australia; should prove to be more common in WA than is apparent.
22. *Goodenia lyrata*	P1; 3K	*ca* 1; 0	MUR	?	?	*G. modesta*	Taxonomically confused with *G. modesta*, requires clarification.
23. *Goodenia modesta*	P3; 3K	*ca* 4; 0	TAN, CR, GSD	?	?	*G. lyrata*	As per *G. lyrata*.

Appendix 1 (cont.)

Taxa	Status * (CALM; ROTAP)	Number of populations (total; in conservation reserves)	WA Distribution (IBRA)	Number of plants (estimated)	Main threats	Closest relative	Notes
24. *Goodenia neogoodenia*	P4; 3R	+.6; *ca* 1	CAR, MUR, YAL	< 1000	mining activities, water point degradation	-	Well surveyed in recent years with a number of populations not vouchered, which should facilitate removal from Priority listings.
25. *Goodenia nuda*	P1; 3K	*ca* 8; 0	PIL	?	mining activities	*G. microptera*	Recently surveyed and found to be more common than previously thought.
26. *Goodenia omearana*	P1; 2K	3; 0	PIL	< 150	mining activities	*G. pascua*	Requires urgent surveys; 2 populations under immediate threat.
27. *Goodenia pallida*	P1; 1K	1; ?	PIL	?		*G. nuda*	No collections at PERTH, requires surveys to relocate only population.
28. *Goodenia pascua*	P3; 3K	*ca* 6; ?	PIL, CAR	?	?	*G. glauca*	Surveys required; poorly known (including taxonomically).
29. *Goodenia perryi*	P3; 1K	6; ?	AW, YAL	< 500	salinity, weeds	*G. incana*	More common than previously thought, although still requiring Priority listing.
30. *Goodenia phillipsiae*	P1; 1K	*ca* 1; 0	ESP	?	?	-	Surveys required to relocate holotype populations.
31. *Goodenia purpurascens*	P3; -	*ca* 3; 0	LSD, NK	?	?	*G. paludicola*	Common in NT and QLD, although very poorly known from WA.
32. *Goodenia quadrilocularis*	P2; 2KC-	*ca* 3; 3	ESP, JF	< 500	?	-	Surveys required to substantiate the Porongurups population.
33. *Goodenia salmoniana*	P1; 1K	1; 0	GAS	?	land clearing	-	Urgent surveys are required to relocate the species (known only from holotype).
34. *Goodenia scapigera* subsp *graniticola*	P2; 2KC-	*ca* 3; 3	MAL	< 150	?	*G. drummondii*	Fully represented on conservation reserves though from only 3 small populations.
35. *Goodenia schwerinensis*	P3; 3K	6; 0	CR, MUR	?	?	*G. glabra*	Known from a wide range.
36. *Goodenia sepalosa* var *glandulosa*	P3; 3K	*ca* 6; 0	DL, NK, VB	?	?	-	Known from a wide range.
37. *Goodenia sericostachya*	P3; 3K	*ca* 5; ?	CAR, GS	< 1000	land clearing	-	Surveys required.
38. *Goodenia* sp Lake King (*M Gustafsson et K Bremer* 132)	P2; 3KC-	3; 2	AW	< 50	salinity, hydrological changes	*G. pinnatifida*	Urgent surveys required; very poorly known.
39. *Goodenia* sp Scaddan (*CD Turley* 41VM/1099)	P1; 2K	2; 0	ESP	< 200	salinity, hydrological changes	*G. claytoniacea*	Urgent surveys required; very poorly known.
40. *Goodenia* sp South Coast (*AR Annels* ARA 1846)	P3; 3K	*ca* 3; 3	JF,WAR	< 200		*G. caerula*	A poorly known species requiring taxonomic study.
41. *Goodenia stellata*	P3; 3KC-	8; ?	MUR, GAS, LSD, PIL	> 1000	mining activities	*G. crenata*	Wide range but still under potential threat.
42. *Goodenia stenophylla*	P4; 2RC-	*ca* 7; *ca* 4	ESP	?		*G. helmsii*	Requires continued monitoring.
43. *Goodenia strangfordii*	P1; -	*ca* 3; 0	GSD, VB	?	water point degradation	*G. fascicularis*	Occurs across NT and into QLD, although poorly known in WA.
44. *Goodenia suffrutescens*	P1; 2K	4; 0	GSD, TAN	?		*G. azurea*	Surveys required.
45. *Goodenia trichophylla*	P2; 3KC-	*ca* 7; ?	ESP, GS, COO, MAL	?	salinity, land clearing	*G. caerula*	Further surveys required.
46. *Goodenia varia*	P2; -	*ca* 3; 0	COO, MAL	?		*G. ovata*	Common across southern Australia.
47. *Goodenia virgata*	P2; -	3; 0	GD; GSD	?		*G. nuda*	Surveys required; also known from NT.
48. *Goodenia xanthotricha*	P1; 3KC-	*ca* 4; *ca* 3	GS, SWA	?		-	Known mostly from historical collections.

* See Table 3 for an explaination of CALM Priority list codes. See Briggs & Leigh (1996) for an explanation of ROTAP codes.

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Effects of short-term drought on the avifauna of Wanjarri Nature Reserve: What do they tell us about drought refugia?

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Abstract

A bird survey in the Wanjarri Nature Reserve in the Goldfields of Western Australia at the end of a year long drought revealed two responses to the short-term dry spell. Firstly, many bird populations were present in very low numbers. Secondly, areas of groving and creekline mulga supported a significantly higher number of bird species and individuals than other habitats. This was thought to be due to the greater foliage cover in groving and creekline mulga, probably as a consequence of soil structure, greater water availability and higher soil fertility. These areas of groving and creekline mulga may be important as drought refugia for resident bird species. Our results need to be confirmed by a more comprehensive study but the identification of drought refugia is of fundamental importance in the conservation of birds in the arid-zone of Australia, so we believe that the conservation of these groving and creekline mulga areas should be given a high priority.

Keywords: birds, drought refugia, mulga, spinifex, foliage cover, conservation, landscape

Introduction

Arid habitats, especially those in Australia, are characterised by the unpredictable nature of resource availability. Rainfall is spatially and temporally erratic and this leads to large fluctuations in faunal biomass and productivity in any particular area (Stafford-Smith & Morton 1990). Birds in the arid-zone adapt to the ephemeral nature of available resources in two ways. The first group, characterised by many honeyeaters, are highly mobile and cover large areas in their search for suitable habitats. Their strategy is to be mobile enough so that they can always find areas of recent rainfall, hence high biomass and productivity, no matter where they occur (Davies 1986). The second group, characterised by thornbills and robins, are resident and relatively non-mobile. Their strategy is to eke out an existence in drought refugia during periods of low rainfall. After heavy rains, populations in the drought refugia increase and move out into previously unsuitable habitat to take advantage of the increased productivity (Davies 1986). During drought, most populations die out and only those located in drought refugia persist. Their survival strategy approximates a "core-satellite" population model (Boorman & Levitt 1973; Hanski 1982) where some habitats that support populations which persist for long periods of time are surrounded by habitats that are occupied only part of the time, usually when conditions are favourable (Harrison 1991).

Conservation and management of the first group of highly-mobile birds within a reserve system is difficult due to the unpredictable nature of their occurrence, both temporally and spatially. Reservation of a particular area will seldom satisfy their conservation needs because the areas they cover are so large. Members of the second group of resident birds are easier to conserve and manage within a reserve system because all their needs can be provided within a relatively small area. One of the main objectives in conserving and managing relatively non-mobile species is to locate and identify their refugia. Drought refugia are likely to be of fundamental importance because they provide the only suitable habitat for these species during dry conditions, so the loss of these areas will lead to local extinction (Davies 1986). It has been postulated that the degradation of relatively fertile drought refugia was largely responsible for the extinction of almost all medium-sized mammals in the arid-zone of Australia (Morton 1990).

In September 1994, we examined patterns of habitat use by birds during a short drought at Wanjarri Nature Reserve (27° 25' S, 120° 40' E; 500 m asl) in the Goldfields region of Western Australia. Wanjarri (53 248 ha) is located within the Murchison Interim Biogeographic Regionalisation for Australia (IBRA) Region (formerly the Austin Vegetation District), which is the second largest IBRA Region in WA (Thackway & Cresswell 1995). Its vegetation, soils and fauna have been affected by pastoral activity. Although the reserve was relinquished as a pastoral lease in 1971, the effects of grazing were still apparent; 75% of the reserve was in 'good' resource condition, 23% in 'fair' and 2% in 'poor' in 1992 (Pringle 1995). Wanjarri is ideal for studies of drought refugia because it is located well within the arid-zone, so patterns found here are likely to be applicable to other arid areas, and results have relevance to both pristine and grazing affected vegetation in the arid-zone. While our results do not provide unequivocal evidence, we believe that the patterns we observed provide a strong indication as to which habitats act as drought refugia.

Methods

Bird censuses were carried out from 30th August to 4th September 1994 between 0730 and 1700 at 21 sites in Wanjarri Nature Reserve. Birds were assessed by the square transect method (Biological Survey Committee 1984). At most sites we set up two 200 x 200 m square grids. Both authors walked the four sides and one diagonal of one square at each site, over approximately 45 minutes, and recorded all birds seen or heard within 30 m of either side of the transect line. On those sites where the habitat features were linear (such as creeklines and breakaways), we conducted counts on two linear 1080 m transects rather than 200 x 200 m squares. At all sites, we added the results from the two censuses. Birds seen or heard outside the 60 meter transect band, or only seen flying overhead, were recorded as opportunistic records. The time at which censuses were conducted in different habitats was randomised with respect to time of day to reduce any bias from variations in bird activity through the day. The counts in 1994 were conducted in what we considered drought conditions, because only 87.4 mm of rain had fallen in the 12 months prior to September 1994 at Albion Downs, 30 km N of Wanjarri (Fig 1). This compares with the average annual rainfall at Albion Downs of 237.8 mm.

Habitats

The 21 sites censused for birds were divided into four broad habitat types; (1) groving and creekline mulga communities (5 sites), (2) open mulga communities (5 sites), (3) spinifex communities (4 sites), and (4) other communities (7 sites). The four community types were defined as follows;

(1) groving and creekline mulga communities: those where mulga (*Acacia aneura*) grew to 10 m in either major shallow drainages, which were up to 350 m wide, or where mulga occurred in discrete groves independent of any co-ordinated drainage. In landscape terms, the drainages formed corridors of denser vegetation between the granite-dominated high points and the lower spinifex plains. Foliage cover was usually around 25-30%. A wide variety of shrubs and grasses were often present, including *Grevillea sarissa*, *Rhagodia eremaea*, *Solanum lasiophyllum* and *Gnephosis foliata*, and dense leaf litter, sometimes redistributed by flooding, was usually a feature of this community type.

(2) open mulga communities: those where mulga was the structurally dominant plant as either a small tree or a shrub. Foliage cover was around 15-20%. A wide variety of lower shrubs or grasses were often present, including *Acacia ligulata*, *Eremophila fraseri*, *Eragrostis eriopoda* and *Aristida contorta*. When *Triodia basdowii* was present, it was relatively uncommon and did not achieve the large clump size that it did on sandier soils.

(3) spinifex communities: those in which *Triodia basdowii* was the dominant plant species and formed a foliage cover of 30-70%. Spinifex communities occurred either on open plains or as a dune/swale sequence. When they occurred on open plains, the overstorey was dominated by either mallees (*Eucalyptus oldfieldii* and *E. leptopoda*) or wattles (*Acacia aneura*, *A. pachyacra* and *A. coolgardiensis*) depending on soil characteristics. When they occurred as a dune/swale sequence, then *E. gongylocarpa*, *Grevillea pterosperma* and *A. ligulata* were the

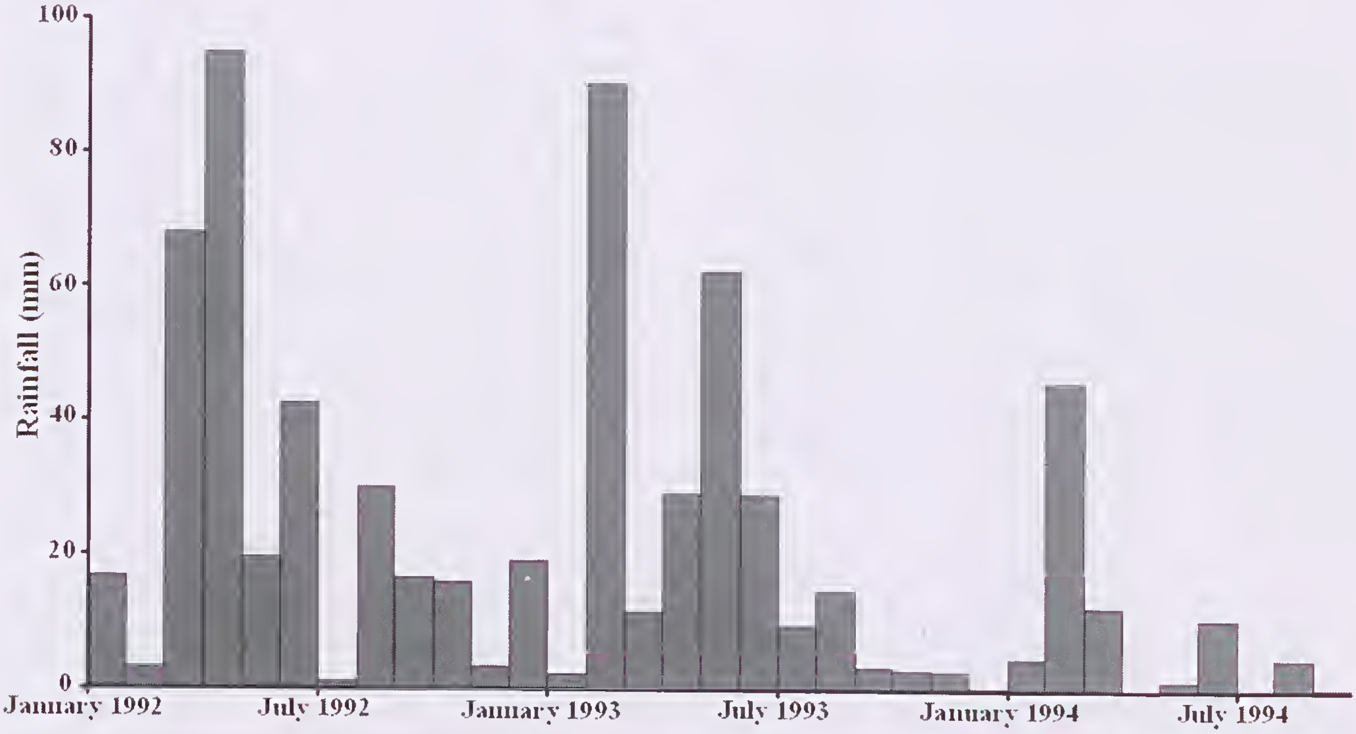

Figure 1. Monthly rainfall data for Albion Downs station about 30 km N of Wanjarri from January 1992 until September 1994. Note that the six months prior to the September 1994 survey were very dry although February 1994 had been relatively wet.

dominant overstorey species on the dune and *Thryptomene maisonneuvii* and *A. coolgardiensis* were the dominant overstorey species in the swale.

(4) other communities: this included a variety of community types that differ greatly from the other three. Examples in this study were riverbeds lined with *E. camaldulensis*, chenopod flats, stony plains and breakaways.

Statistical analyses

The number of species and individuals recorded per site was compared using a one-way ANOVA with Fisher's PLSD for post-hoc testing. Analyses were conducted using SuperANOVA 1.11 (Abacus Concepts 1993). The α–value for significance was 0.05.

Results

A total of 38 species was recorded during the bird transects in September 1994 (Table 1), comprising 293 individuals at an average of 9.3 birds person hr^{-1}. Some species, such as Chestnut-rumped Thornbill, Yellow-rumped Thornbill and Southern Whiteface (see Table 1 for scientific names), managed to maintain relatively high numbers despite the dry conditions. However, the overall pattern was for low numbers, especially among nomadic species and raptors.

The number of species recorded differed significantly ($F_{3,17} = 5.33$, $P = 0.009$) between the four habitat groups (Table 2). Areas of groving and creekline mulga supported a significantly higher number of species than the other habitat groups, although there was no significant difference between the number of species in the remaining three habitat groups (Table 1). The number of individuals also differed significantly ($F_{3,17} = 5.37$, $P = 0.009$) between the four habitat groups (Table 2). Again, the number of individuals in groving and creekline mulga were significantly higher than the other three habitat groups which between them showed no significant difference (Table 2).

Table 1

Numbers of individual species recorded in each of four habitats at Wanjarri Nature Reserve. Values are the mean number of individuals per site (± se for species where n > 2; n is the total number of individuals sighted on all sites).

Species	n	Groving mulga (5 sites)	Open mulga (5 sites)	Spinifex (4 sites)	Other (7 sites)
Brown Falcon (*Falco berigora*)	1	0	0	0.25	0
Nankeen Kestrel (*Falco cenchroides*)	1	0	0	0	0.14
Common Bronzewing (*Phaps chalcoptera*)	2	0.40	0	0	0
Galah (*Cacatua roseicapilla*)	10	1.40 ± 1.17	0	0	0.43 ± 0.43
Port Lincoln Ringneck (*Barnardius zonarius*)	9	0.60 ± 0.40	0	0	0.86 ± 0.86
Tawny Frogmouth (*Podargus strigoides*)	2	0	0	0	0.29
Red-capped Robin (*Petroica goodenovii*)	5	0.60 ± 0.24	0	0	0.29 ± 0.18
Hooded Robin (*Melanodryas cucullatus*)	4	0.20 ± 0.20	0	0	0.43 ± 0.43
Rufous Whistler (*Pachycephala rufiventris*)	3	0.40 ± 0.24	0.20 ± 0.20	0	0
Grey Shrike-thrush (*Colluricincla harmonica*)	1	0.20	0	0	0
Crested Bellbird (*Oreoica gutturalis*)	8	0.40 ± 0.40	1.00 ± 0.77	0	0.14 ± 0.14
Willie Wagtail (*Rhipidura leucophrys*)	6	0.20 ± 0.20	0.60 ± 0.60	0	0.29 ± 0.29
Chestnut-breasted Quail-thrush (*Cinclosoma castaneothorax*)	4	0	0	0	0.57 ± 0.57
Grey-crowned Babbler (*Pomatostomus temporalis*)	9	0	1.80 ± 1.80	0	0
White-browed Babbler (*Pomatostomus superciliosus*)	6	1.20 ± 1.20	0	0	0
Unidentified Fairy-wren (*Malurus* sp.)	3	0.60 ± 0.60	0	0	0
Rufous-crowned Emu-wren (*Stipiturus ruficeps*)	1	0	0	0.25	0
Striated Grasswren (*Amytornis striatus*)	1	0	0	0.25	0
Weebill (*Smicrornis brevirostris*)	1	0	0	0.25	0
Inland Thornbill (*Acanthiza apicalis*)	9	1.00 ± 0.77	0.20 ± 0.20	0.25 ± 0.25	0.29 ± 0.29
Slaty-backed Thornbill (*Acanthiza robustirostris*)	13	2.40 ± 1.03	0	0	0.14 ± 0.14
Chestnut-rumped Thornbill (*Acanthiza uropygialis*)	70	7.00 ± 1.64	0.40 ± 0.40	1.75 ± 1.75	3.71 ± 0.97
Yellow-rumped Thornbill (*Acanthiza chrysorrhoa*)	24	1.00 ± 0.45	0.40 ± 0.40	0	2.43 ± 1.66
Southern Whiteface (*Aphelocephala leucopsis*)	17	3.00 ± 0.95	0	0	0.29 ± 0.29
Varied Sittella (*Daphoenositta chrysoptera*)	5	1.00 ± 1.00	0	0	0
White-browed Treecreeper (*Climacteris affinis*)	8	1.60 ± 0.93	0	0	0
Yellow-throated Miner (*Manorina flavigula*)	11	1.40 ± 0.98	0.20 ± 0.20	0.75 ± 0.75	0
Singing Honeyeater (*Lichenostomus virescens*)	6	0.40 ± 0.24	0.20 ± 0.20	0	0.29 ± 0.29
Grey-fronted Honeyeater (*Lichenostomus plumulus*)	7	0	0	1.75 ± 1.18	0
White-fronted Honeyeater (*Phylidonyris albifrons*)	4	0	0.20 ± 0.20	0	0.43 ± 0.43
Zebra Finch (*Poephila guttata*)	1	0	0	0	0.14
Black-faced Woodswallow (*Artamus cinereus*)	25	0	4.00 ± 1.82	0	0.71 ± 0.71
Grey Butcherbird (*Cracticus torquatus*)	2	0.20	0.20	0	0
Pied Butcherbird (*Cracticus nigrogularis*)	8	0.20 ± 0.20	0.40 ± 0.40	0	0.71 ± 0.47
Australian Magpie (*Gymnorhina tibicen*)	1	0	0.20	0	0
Little Crow (*Corvus bennettii*)	7	0	1.40 ± 1.40	0	0
Torresian Crow (*Corvus orru*)	1	0	0.20	0	0

Table 2

Number of species and individuals recorded in each habitat group for Wanjarri Nature Reserve. Values are mean ± se; *n* is the number of sites in each habitat group; values with different superscript letters are significantly different.

Habitat type	*n*	# of species	# of individuals
Groving or creekline mulga	5	8.60 ± 1.50^a	25.00 ± 3.39^a
Open mulga	5	3.60 ± 1.50^b	11.80 ± 4.79^b
Spinifex	4	2.25 ± 0.95^b	5.25 ± 2.10^b
Other communities	7	3.86 ± 0.74^b	12.57 ± 2.44^b

Table 3

Numbers of raptors and all birds sighted during this study at Wanjarri Nature Reserve, compared to Hall *et al.* (1994). All values are number of individuals sighted per person hour.

	This study	Hall *et al.* (1994)		
	September 1994	February 1979	May 1980	August 1981
Raptors	0.06	0.28	0.48	0.92
All birds	9.3	17.3	23.4	37.4

Discussion

The data obtained in this survey at Wanjarri Nature Reserve support two notable aspects of faunal response to short-term dry conditions. The first aspect is that the number of bird species and individuals was low during the drought conditions of our study. Although we recorded most resident passerine species in the reserve (Moriarty 1972), the number of individuals that we recorded (Table 3) was low compared to the intensive study of the reserve conducted by Hall *et al.* (1994), even though we recorded all the resident passerine species they did. In addition, the number of raptors that we sighted (Table 3) was also low compared to Hall *et al.* (1994). Additional evidence of stress was the absence of breeding records during the survey, despite the survey having been conducted at a time when many species would be expected to breed. These observations suggest that that biological productivity was low during the drought conditions of our study.

The second aspect was that the decline in avian species richness and abundance at Wanjarri differed considerably between groving/creekline mulga and other habitats. Areas of groving and creekline mulga supported a much higher number of birds, both species and individuals, than the other habitats. This suggests that these areas act as drought refugia for resident birds during drought conditions. The 14 bird species that were most common in groving and creekline mulga (Table 1) are considered to be resident (Blakers *et al.* 1984; Higgins 1999; Higgins *et al.* 2001). They include nine species that can be reliably recorded in mulga communities across Australia (Galah, Red-capped Robin, Rufous Whistler, Grey Shrike-thrush, White-browed Babbler, Inland Thornbill, Chestnut-rumped Thornbill, Southern Whiteface and Singing Honeyeater) and four species that are considered peripheral in mulga communities (Common Bronzewing, White-browed Treecreeper, Yellow-throated Miner and Slaty-backed Thornbill; Cody 1994). The high numbers of bird species and individuals recorded from groving and creekline mulga communities in this study were in sharp contrast to the spinifex-dominated habitats.

So what are the habitat characteristics and parameters of groving and creekline mulga that allow birds to persist there in dry conditions? The most obvious characteristic is that they have a much greater vegetation density than other habitats. The five creekline and groving mulga communities had an average of 25 to 30% foliage cover, whereas open mulga communities had an average of only 15 to 20% (H Pringle, Department of Agriculture, unpublished data). Groving and creekline mulga areas probably have greater vegetation density than other habitats because of differences in soil structure and the greater availability of water and nutrients. In contrast to open mulga soils, the soils of groving and creekline mulga areas usually have a shallow A horizon and subsequent horizons in the same texture group as the A horizon leading to less resistance to root penetration (P Hennig, Department of Agriculture, unpublished data). In addition, soils of groving and creekline mulga have stable macropores that enable them to absorb up to 10 times the amount of water of open mulga soils (Greene 1992). This greater water availability is accentuated because groving and creekline mulga occupies low points in the landscape, where water and nutrients tend to collect (Tongway 1990; Tongway & Ludwig 1990; Ludwig *et al.* 1994). In contrast, open mulga communities tend to occur on hardpans and breakaway footslopes where there is less water and nutrients (Tongway & Ludwig 1990; Greene 1992; Ludwig *et al.* 1994). So, plants that grow in areas of groving and creekline mulga have greater access to water and nutrients and can form a denser canopy. Their access to water and nutrients also means that they can maintain greater productivity during dry periods, which presumably supports more invertebrates and, hence, insectivorous birds. It has been shown that areas of groving and creekline mulga support higher densities of terrestrial invertebrates than other habitats (Whitford *et al.* 1992; Noble *et al.* 1996), which may be important as many mulga-inhabiting birds forage on the ground (Recher & Davis 1997). Unfortunately, no comparable information is available on the arboreal invertebrate fauna.

Morton (1990) proposed that vertebrates in arid-zone ecosystems, especially mammals, were dependent on "uncommon pockets of relatively fertile, moist country that are scattered across the arid-zone" to act as refugia in times of drought. The significance of this to the conservation and management of arid-zone vertebrates is that the degradation of these drought refugia, by feral or introduced herbivores, changed fire regimes, or predation by introduced mammals, could cause species extinction. Indeed, Morton (1990) proposed that degradation of drought refugia could explain the extinction of large numbers of medium-sized mammals in the arid-zone. Although extinctions in the arid-zone have only occurred among mammal species, there are some indications that we may see loss of biodiversity among the arid-zone avifauna in the near future (Recher & Lim, 1990; Smith *et al.* 1994; Recher 1999). Thus, identification of drought refugia is imperative if we are to maintain avian biodiversity in Australia's arid-zone. To unequivocally identify drought refugia for birds in the arid-zone of Australia, a long-term monitoring project is needed to assess the abundance of birds in all habitats within a landscape and observe how abundance varies when drought periods occur. As far as we are aware, no study of the arid-zone of Australia has yet been conducted over a wide enough range of habitats for a sufficiently long time period to unequivocally identify drought refugia. As our study only used data from a dry period, it cannot provide unequivocal evidence of avian drought refugia. However, the patterns we observed strongly suggest that areas of groving and creekline mulga act as drought refugia for resident arid-zone birds, so there should be a strong focus in arid-zone management to conserve areas of groving and creekline mulga unless a more comprehensive study refutes our findings.

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Characteristics of Marri (*Corymbia calophylla*) fruits in relation to the foraging behaviour of the Forest Red-tailed Black Cockatoo (*Calyptorhynchus banksii naso*)

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Abstract

Forest Red-tailed Black Cockatoos (*Calyptorhynchus banksii naso*) feed predominantly on seeds of the eucalypt Marri (*Corymbia calophylla*) and often only from specific feed trees. There was no difference between wet weight of fruits from feed (24.1 ± 1.72 g) and non-feed trees (23.2 ± 1.57 g), but trees from which Forest Red-tailed Black Cockatoos fed had a significantly higher seed number per fruit (3.9 ± 0.18), a greater individual dry seed weight (0.10 ± 0.003 g) and total seed weight per fruit (0.39 ± 0.02 g), and a higher ratio of total seed dry weight to fruit wet weight (0.02 ± 0.001) compared with non-feed trees (3.1 ± 0.20 seeds per fruit; 0.09 ± 0.005 g individual seed dry weight; 0.29 ± 0.020 g total seed dry weight per fruit; 0.013 ± 0.001 ratio of total seed dry weight to fruit wet weight). Discriminate analysis had a limited capacity to predict Marri use by Forest Red-tailed Black Cockatoos, correctly classifying about 70 % of feed trees. Seed number and total seed mass were the best fruit characteristics for the prediction of tree type. We conclude that Forest Red-tailed Black Cockatoos selectively forage from trees with fruits that have a high seed yield, but the method by which the cockatoos select these trees is unclear.

Key words: cockatoo, marri, food selection, seeds, parrots, eucalyptus

Introduction

The Forest Red-tailed Black Cockatoo (*Calyptorhynchus banksii naso*) inhabits tall eucalypt forests of Marri (*Corymbia calophylla*), Jarrah (*Eucalyptus marginata*) and Karri (*E. diversicolor*) in the south-west of Western Australia (Saunders *et al.* 1985; Saunders & Ingram 1995; Johnstone & Kirkby 1999). The geographical distribution and abundance of this sub-species of Red-tailed Black Cockatoo is suspected to have declined over the past 50 years (Saunders & Ingram 1995); it is considered to be rare to uncommon throughout its range (Johnstone & Storr 1998; Johnstone & Kirkby 1999), and is listed as near threatened (Garnett & Crowley 2000).

The Forest Red-tailed Black Cockatoo feeds on seeds of a variety of species of native flora, including Jarrah, Karri, Blackbutt (*E. patens*), Albany Blackbutt (*E. staeri*), Common Sheoak (*Allocasuarina fraseriana*) and Snottygobble (*Persoonia longifolia*), but Marri seeds are its principal food source (Johnstone & Kirkby 1999). Flocks appear to select specific Marri trees when feeding, returning to the same tree until its food supply is exhausted and often ignoring neighbouring trees. Johnstone & Kirkby (1999) suggested that the quality of the fruit varies between trees selected and ignored by these cockatoos, and that the quality of food might limit the breeding success and long-term distribution and abundance of Forest Red-tailed Black Cockatoos. Cooper (1999) reported that the fruits of feed trees had a higher seed yield than non-feed trees. We examine here fruit characteristics (fruit mass, seeds per fruit and seed mass) to further determine differences between fruits of feed and non-feed Marri trees of the Forest Red-tailed Black Cockatoo.

Methods

Fruits from feed and non-feed Marri trees of the Forest Red-tailed Black Cockatoo were examined at Armadale, Jarrahdale and north of the North Dandalup Dam, south-east of Perth, Western Australia (31° 58′ S, 115° 51′ E), in 1999 and 2003. Feed trees were identified either by observing birds feeding from a particular tree, or by observing freshly chewed fruits scattered at the base of the tree. Non-feed trees had no fruits opened and discarded by Forest Red-tailed Black Cockatoos beneath them. Three other species of parrot also feed on these Marri fruits, Baudin's Cockatoo (*C. baudinii*), Carnaby's Cockatoo (*C. latirostris*) and the Red-capped Parrot (*Purpureicephalus spurius*). Each species leaves characteristic marks on discarded fruits (Cooper 1999, 2000), and so trees from which the Forest Red-tailed Black Cockatoo had been feeding could be easily identified.

Six fruits were collected from each feed tree and from the nearest non-feed tree using long-handled clippers.

We attempted to take the six fruits from different parts of each tree. Fruit wet mass, fruit length and diameter, seed number and total seed dry mass were recorded for each fruit. Seeds were dried to a constant weight at 50-70 °C in a Labmaster drying oven. Feed and non-feed comparisons were made using nested ANOVA (SPSS version 11.5), with year and tree type as fixed factors, and site as a random factor nested within year. Classificatory discriminant analysis was accomplished with *statistiXL* (v 1.1). Mean (± S.E.) values for feed and non-feed trees were calculated from the mean values for six fruits from each tree.

Results

Feed tree fruits were significantly longer ($F_{1,338} = 14.48$, $p < 0.001$) and had a greater diameter ($F_{1,338} = 11.65$, $p = 0.001$); they also had more seeds ($F_{1,337} = 24.3$, $p < 0.001$), larger seeds ($F_{1,323} = 10.2$, $p = 0.002$) and a higher total dry seed mass ($F_{1,333} = 40.4$, $p < 0.001$) than non-feed trees (Table 1). The ratio of total seed mass to fruit wet mass was also significantly higher for fruits from feed than from non-feed trees ($F_{1,335} = 46.44$, $p < 0.001$). Wet mass of the fruits did not differ significantly between feed and non-feed trees ($F_{1,335} = 3.3$, $p = 0.070$). Year of sampling did not affect the fruit length ($F_{1,29} = 2.80$, $p = 0.105$), the seed content of fruits (either seed number, $F_{1,29} = 0.45$, $p = 0.506$; individual seed mass, $F_{1,30} = 2.32$, $p = 0.139$; or total dry seed mass, $F_{1,29} = 1.69$, $p = 0.204$), or the ratio of total seed mass to fruit wet mass ($F_{1,29} = 1.89$, $p = 0.180$), but the wet mass of whole fruits ($F_{1,29} = 7.97$, $p = 0.009$) and fruit diameter ($F_{1,29} = 9.58$, $p = 0.004$) were significantly greater in 2003. All fruit and seed characteristics showed highly significant variation between sites: fruit wet mass ($F_{29,335} = 31.7$, $p < 0.001$), fruit length ($F_{29,338} = 16.21$, $p < 0.001$), fruit diameter ($F_{29,338} = 28.63$, $p < 0.001$), seed number ($F_{29,337} = 2.64$, $p < 0.001$), individual seed mass ($F_{29,323} = 2.31$, $p < 0.001$), total seed mass ($F_{29,333} = 2.92$, $p < 0.001$), and the ratio between the total seed mass to fruit wet mass ($F_{29,335} = 6.18$, $p < 0.001$).

Table 1

Characteristics of Marri fruits from trees that Forest Red-tailed Black Cockatoos use (Feed) and ignore (Non-feed). Values are mean ± standard error, n = 31, average of 6 fruits per tree. * indicates significant difference at $p < 0.05$.

	Feed	Non-feed
Fruit wet mass (g)	24.1 ± 1.72	23.2 ± 1.57
Seed number per fruit*	3.9 ± 0.18	3.1 ± 0.20
Individual seed dry mass (g)	0.10 ± 0.003	0.09 ± 0.005
Total seed dry mass (g) *	0.39 ± 0.018	0.29 ± 0.020
Total seed mass to fruit mass ratio *	0.02 ± 0.001	0.013 ± 0.001

Discussion

Characteristics of Marri fruits

The characteristics of Marri fruits examined in this study are generally typical of Marri fruits examined in previous studies. Gill *et al.* (1992) reported that Marri fruits contained similar numbers of seeds per fruit (3.1 ± 1.3) as found in this study (3.5 ± 0.2), while Abbott (1984) found an average of 4 seeds per fruit. These slight differences in average number of seeds per fruit are presumably due to variations in study sites and perhaps variation in Marri flowering and fruiting from year to year (Mawson 1995), although we found no differences in seed characteristics between two years. Gill *et al.* (1992) reported that Marri fruits contained a total seed weight of 0.51 ± 0.17 g per fruit compared to 0.34 (± 0.02) g in this study. Again, different localised climatic and soil conditions, and yearly variations in fruiting may account for these differences, although we found no significant difference between the two years sampled.

Two non-feed trees in this study were found to have fruits containing no seeds (classified as male fruits), as has been described previously for Marri (Carr *et al.* 1971; Mawson 1995). Marri varies with respect to the proportion of male fruits. Some trees only produce male fruits, never female fruits containing seeds (Carr *et al.* 1971); male fruits are often withered in appearance, but fruits of the male trees from this study were normal in appearance. According to Carr *et al.* (1971) male fruits have no seeds because of ovule abortion late in development. Mawson (1995) suggested that the presence of male trees meant that birds feeding on Marri need to be discerning, to avoid wasting time and energy feeding on fruits that would give no energetic return. We found that Forest Red-tailed Black Cockatoos are even more discerning, since feed and non-feed trees differ in fruit energy yield.

Feed and non-feed Marri trees

Our study supports Johnstone & Kirkby's (1999) hypothesis that there is a difference in seed characteristics between feed and non-feed Marri trees. Feed trees have a higher seed number, individual seed mass and total seed dry mass per fruit compared with non-feed trees, indicating that cockatoos select Marri trees that have fruits with a higher energy content. Marri seeds contain 22.9 kJ of combustible energy g^{-1} (Cooper *et al.* 2002). Therefore, feed trees provide 8.85 kJ $fruit^{-1}$ (0.39 g x 22.9 kJ g^{-1}; assuming that all the seeds are eaten), which is a 34% greater return than for non-feed trees (6.61 kJ $fruit^{-1}$; 0.29 g x 22.9 kJ g^{-1}).

Clout (1989) and Pepper *et al.* (2000) reported that Glossy Black Cockatoos (*C. lathami*) in New South Wales and South Australia also selected feed trees with a greater seed return than non-feed trees, when feeding on *Allocasuarina littoralis* and *A. verticillata* respectively. Feed *A. verticillata* trees for South Australian Glossy Black Cockatoos (*C. l. halmaturinus*) have 23% larger seeds, 21% more seed per cone and 13% more energy per cone than trees from which the birds did not feed (Pepper *et al.* 2000). In our study, feed Marri trees had 10% larger seeds and 25% more seeds per fruit than non-feed trees and provided Forest Red-tailed Black Cockatoos with 34% more energy per fruit than non-feed trees (2.6 times the energy difference for *A. verticillata*). This presumably reflects the large size of Marri compared to *A. verticillata* seed, and possibly a greater variation of total seed dry mass in Marri compared with *A. verticillata*. It is also possible that Forest Red-tailed Black Cockatoos are more selective feeders than South Australian Glossy Black Cockatoos.

Clout (1989) suggested that *Allocasuarina* feed trees used by Glossy Black Cockatoos had a higher ratio of seed mass to fruit mass than non-feed trees, which indicates reduced handling costs compared to energy gain. For Forest Red-tailed Black Cockatoos there was also a significant difference in the ratio of total seed mass to fruit wet mass. Therefore the cockatoos receive higher energy returns for an equivalent effort by selecting trees with higher energy yields per fruit.

Johnstone & Kirkby (1999) found that wild Forest Red-tailed Black Cockatoos take up to 2.45 minutes to remove, husk and eat the seeds from a Marri fruit. When feeding from feed trees at this rate, they would obtain 3.6 kJ min^{-1}, compared with 2.70 kJ min^{-1} from non-feed trees. The 25% greater feeding rate that Forest Red-tailed Black Cockatoos attain by selecting feed rather than non-feed trees is considerably higher than the 14% increase reported for South Australian Glossy Black Cockatoos (Pepper *et al.* 2000). This increased rate of energy acquisition from feed trees would translate into a reduced daily feeding time or an increased daily energy intake.

South Australian Glossy Black Cockatoos needed to feed for 6 h 24 min day^{-1} to meet their predicted field energy requirements of 626 kJ (Pepper *et al.* 2000). Forest Red-tailed Black Cockatoos have a predicted daily field energy requirement of 934 kJ (Cooper *et al.* 2002), so when feeding from feed trees they would require only 5 h 11 min to obtain this energy, but would require 6 h 29 min day^{-1} for non-feed trees. The ability of these cockatoos to discriminate between Marri with high and low seed yields enables them to greatly reduce their foraging time and increase their energy intake. Decreasing the time required to meet their daily energy demands is of particular importance during the breeding season when the cockatoos have to meet the additional energy requirements of a chick as well as themselves. This is particularly important because the ability to obtain sufficient food, especially when breeding, is a major factor limiting the reproductive success of cockatoos (Saunders *et al.* 1985; Johnstone & Kirkby 1999; Pepper *et al.* 2000).

Predicting Marri seed yield

How the cockatoos determine which trees have the highest seed yield is unclear. Pepper *et al.* (2000) suggest that experience may play an important role in feed tree selection for South Australian Glossy Black Cockatoos feeding on *Allocasuarina*. Visual cues may indicate the potential energy yield of cones/fruits to experienced birds. Pepper *et al.* (2000) suggested that the external morphology of *Allocasuarina* cones may indicate the internal seed content, although Clout (1989) found no difference in cone size (mass, length or width) between feed and non-feed trees. For Marri, there was no visible indication to us in either shape or colour of fruits from feed and non-feed trees. Despite this, there were measurable differences in fruit length and diameter, and seed number, individual mass and total mass, of fruits from feed and non-feed trees. However, these differences were related to site variability for all fruit and seed characteristics, and year to year variability in fruit wet mass and diameter. The flowering/fruiting cycle of Marri occurs on a three to five year cycle, with flowering and fruiting varying greatly from one year to the next (Robinson 1960; Mawson 1995; Johnstone & Kirkby 1999). A feed tree with a high fruit yield in one year requires at

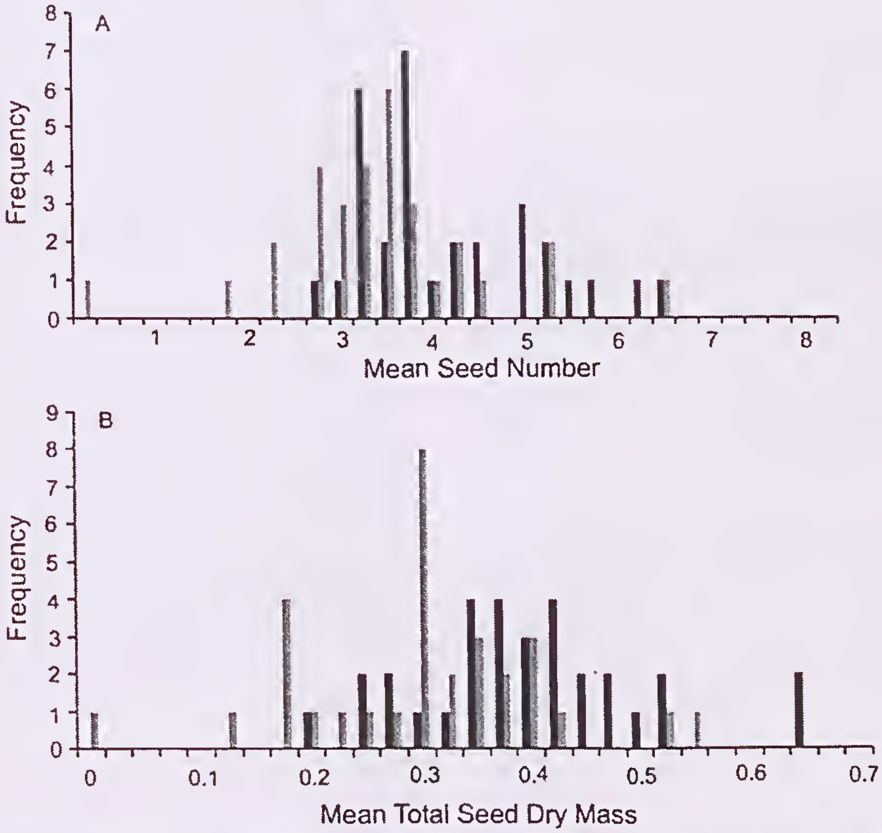

Figure 1. Frequency distribution of seed number (A) and total seed dry mass (g; B) for feed (dark bars; n = 31) and non-feed (light bars; n = 31) Marri trees (means for 6 fruits from each tree).

least three years to replenish sufficient resources to fruit successfully again (Mawson 1995; Johnstone & Kirkby 1999). Therefore, the cockatoos can't simply feed from the same trees each year; they must somehow assess the energy yield of the fruits from individual trees each time they fruit. Either they must reassess a tree each time it fruits, or remember trees with a high yield from the previous fruiting (if indeed high seed yield trees remain so in successive fruitings).

It is important for the future management of these cockatoos that we are able to predict which are feed or non-feed Marri trees. Therefore we examined the possibility of categorising feed and non-feed trees from fruit and seed characteristics, independent of site and year influences. As we measured 6 fruits per tree, we used the mean value for each characteristic for each tree to avoid pseudo-replication. There were no differences (by t-test) between feed and non-feed trees with respect to fruit wet mass ($p = 0.710$), length ($p = 0.781$), or diameter ($p = 0.652$). However, there were highly significant differences (by t-test) between feed and non-feed trees with respect to seed number ($p = 0.006$) and total seed mass ($p = 0.001$). The individual seed mass did not differ significantly ($p = 0.155$), indicating that the differences mainly reflected the number of seeds rather than their individual mass. Although it is possible on a statistical basis to distinguish samples of feed and non-feed trees, it is more difficult to categorise a single tree as feed or non-feed because there is considerable overlap in both seed number and total seed mass between feed and non-feed trees (Fig 1). A discriminant analysis for categorising fruits (using averages of 6 fruits for each tree), based on number of seeds (n) and total seed mass (m, in grams), since these were the two most useful characteristics for discrimination, yielded the following two discriminate functions;

$$F_N = 1.992\,n + 17.454\,m - 7.912$$

$$F_F = 2.040\,n + 8.622\,m - 5.096$$

These functions can be used to classify samples for a further tree by substituting its values for n and m (averages for a sample of 6 fruits); which ever function value is higher categorises the tree as feed (F_F) or non-feed (F_N). The functions correctly classified 71% of feed trees and 68% of non-feed trees. However, the practical application of the identification of potential feed trees is limited by the variability in Marri fruiting on a year to year basis (Mawson 1995). Therefore, habitat trees can't be selected due to their status as feed trees in a particular year. Further study is required to determine patterns of feed tree use over a longer period of time.

This study suggests that Forest Red-tailed Black Cockatoos select trees for a higher energy yield per fruit, and provides a method for prediction of whether a Marri is a feed or non-feed tree in any particular year. However, it is important for further studies to determine how frequently individual trees are used, and how patterns of feeding from particular trees reflect the three to five year Marri fruiting cycle. Further investigation is also required to determine the number of different feed trees used in a particular area over a longer time period, and the total number of trees used by individual flocks of Forest Red-tailed Black Cockatoos.

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Obituary: F G W Jones MA, ScD, CBiol, FIBiol

1914 – 2003

Frederick George William Jones (Fred) was born 'upstairs in the front room' on November 15th 1914 in Cannock, Staffordshire in England, and spent his childhood days nearby in a small coalmining village called Norton Canes in the English 'Black Country'. His first recollection of his father George was in 1918, when George returned from the First World War with serious war wounds, including only one eye. Post war times were hard indeed – Fred had rickets (vitamin D deficiency) and survived pneumonia – but his strong will and sense of purpose was evident from early on, and through his own efforts and hard work, and the encouragement of his mother Alice, he obtained scholarships to attend Queen Mary's Grammar School (1926-1933) in Walsall, Staffordshire, and a State Scholarship to Cambridge University to study Natural Sciences in 1933. It was with some trepidation that he arrived at Jesus College in Cambridge, wearing working boots and with a strong Midlands accent. Nevertheless he flourished both in his studies and in his many other interests – he sang in Jesus College Choir, joined the University Music Society, was a founding member of the University Rambling Club, and secretary of the Botanical Section of the University Natural History Society. He didn't have enough money for the train fare home, so he had to cycle back to the Midlands, and he subsequently cycled all over Britain. Fred graduated in 1937 with a specialisation in Entomology and Experimental Zoology.

Fred's first job (1937 – 1947) was in the Agricultural Advisory Service based in the School of Agriculture in Cambridge. During this era he spent much time working in the Fenlands region of East Anglia advising farmers on how to control damaging agricultural pests and stabilise crop production. Legislation in 1943 enforcing crop rotation in the fenlands ('the Sugar Beet Eelworm Order') was one notable outcome of his work during this period. This early advisory experience gave him a broad background in practical agriculture that benefited him greatly in his later years as a more specialised agricultural scientist. He was in a 'reserved' profession during the Second World War because of the importance of self self-sufficiency in food. As an 'Intelligence Officer' in the Home Guard he had many hilarious (and some serious) tales of the second World War years – such as the inadvertent shooting of the Professor of French in the bottom on maneuvers, and looking out of the window in the Zoology Department to see a Messerschmitt warplane strafing Downing Street in Cambridge. In 1940, he married fellow student Margaret Barnes who studied the same courses as he did and also specialised in entomology, and they had four children (Susan, Roger, Michael and Robert).

From 1947 to 1955, Fred was first a Demonstrator then Senior Lecturer in agriculture at Cambridge University, and Director of Studies in agriculture at Jesus College. His lectures covered the full spectrum of agricultural pests, and later these lectures formed the basis of the textbook *Pests of Field Crops* that he authored jointly with Margaret. He built a successful research team in entomology and Nematology at Cambridge, specialising in later years in Nematology –unsegmented roundworms that attack plant roots. Although beet cyst-nematode became the main focus of his research, other achievements at that time included the discovery and description of the carrot cyst-nematode. In 1948 the family moved to the village of Great Shelford, where Fred ran his two acre garden with agricultural precision, kept honey bees, chickens, ducks and rabbits, and grew more than sufficient vegetables and fruits to feed the family. In 1956 the family moved to Harpenden, Hertfordshire, when Fred was appointed Head of the Nematology Department at Rothamsted Experimental Station, eventually becoming Deputy Director in 1966. He retired officially from Rothamsted in 1979 at age 65, but remained on site until 1987 as an honorary scientist in the Statistics Department. After retiring, Fred maintained his scientific activities, first as editor of *Nematologica*, then as Managing Director and Secretary of the International Trust for Zoological Nomenclature (1980-1987).

The time when Fred was at Rothamsted was the heyday of the Nematology Department. Fred made many valuable contributions to this subject, including the first steps in breeding potatoes resistant to the potato cyst-nematode, proposing a gene-for-gene interaction between cyst nematodes and their hosts, developing an understanding of the soil as an environment for nematodes, and significant contributions to modelling, population dynamics, population genetics, and other aspects of cyst and other nematodes. Fred was blessed with common sense, clear vision and sense of purpose, and was very practical in all that he did. He always used time efficiently and prided himself on effective chairing of meetings. He also made a point of injecting humour into otherwise dull scientific reports and correspondence, and into his talks and lectures.

In addition to three editions of *Pests of Field Crops*, he wrote over two hundred scientific papers and ran many courses in Plant Nematology locally and overseas. He was also an external examiner for various universities, a Visiting Professor at Imperial College, London University, an editor of various scientific journals and a member of many visiting groups and national committees. He mentored many younger scientists. Fred also travelled widely for work – to north and south America, the Caribbean, Europe, Australia and India. He spent considerable time in India, and ran the first Plant Nematology course there at Aligarh Muslim University and later another at the Indian Agricultural Research Institute in New Delhi. He was the first to discover the potato cyst-nematode in India (in the Nilgiris), which did much to foster the establishment of Plant Nematology in India, and supported training of Indian nematologists.

Fred's work was recognised in many ways – for example by the award of an ScD degree from Cambridge University in 1969, and Honorary Fellowships by the Society of Nematologists, the European Society of Nematologists, the Afro-Asian Society of Nematologists, the Institute of Biology and the Association of Applied Biologists. He was President of the Association of Applied Biologists in 1973-74. Ever the individualist, he declined the OBE offered on his retirement from Rothamsted. Throughout this time Fred maintained his interest in singing, *e.g.* as a member of the St. Albans Bach Choir and the Lea Singers, and he was responsible for the annual 'Music for a Summers Evening' held at Rothamsted Manor each year. He also took up skiing as a hobby during his 50's.

After leaving Harpenden in 1987 Fred returned briefly to his roots in the Staffordshire 'Black Country'. Then, in 1991 he moved to Perth in Western Australia, where two of his sons worked. Because of his role in helping to father Nematology in India, in 1992 at the age of 78, he also travelled alone to India as an invited guest to attend the first meeting of the Afro-Asian Society of Nematologists in Aligarh where he was made an honorary fellow of the Society. This was the last major international scientific meeting at which he spoke.

Fred's wife Margaret died suddenly in 1980. Following a second marriage and divorce, he married Marjorie Sutton in Staffordshire, who died of cancer in 1988. After he had moved to Australia he married Enid Moore in 1994 (Fred, Margaret and Enid had been fellow students in their university days). Fred and Enid both continued to pursue scientific and botanical interests - membership of the Royal Society of Western Australia (where they sat in the front row and asked searching questions), Friends of Kings Park and Botanic Gardens, and the local Cambridge Society, and indulged their passion for the unique native flora of Western Australia. Fred also sang in the local church choir. He travelled widely in Australia and went back to Europe several times despite being well into his 80's.

Three years ago Fred was diagnosed with heart disease which slowed him down physically but not mentally: during this time he was greatly supported by Enid, now aged 90. He died on 12th September 2003 in the South Perth Community Hospital in Western Australia. His wife Enid, three sons and a daughter, eight grandchildren, and one great grandchild survive Fred.

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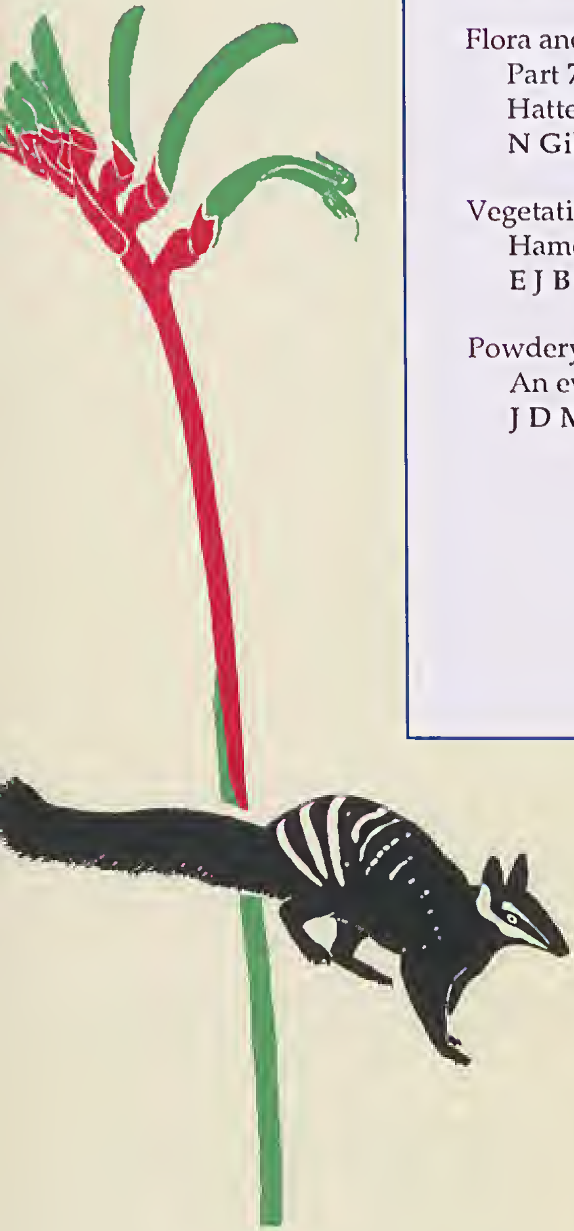

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Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor). The Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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GPS-geodetic deformation monitoring of the south-west seismic zone of Western Australia: review, description of methodology and results from epoch-one

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Abstract

The south-west seismic zone (SWSZ) is a northwest-southeast trending belt of intraplate earthquake activity that occurs in the south-western corner of Western Australia, and is one of the most seismically active areas in Australia. Since the SWSZ lies as close as ~150 km from the ~1.4 million population of the Perth region, it poses a distinct seismic hazard. Earthquake activity recorded by Geoscience Australia over the past three decades suggests that the SWSZ could be deforming by 0.5-5 mmy^{-1}. However, little is currently known about the magnitude and orientation of this deformation, and whether there is any associated surface expression. Previous geodetic studies of the SWSZ that used both terrestrial and Global Positioning System (GPS) techniques are inconclusive, due mainly to the imprecision of the technologies used in relation to the likely small amount of any surface deformation. Therefore, a new 48-point GPS-geodetic monitoring network has been established across the SWSZ to attempt to detect surface deformation, for which epoch-one episodic GPS-geodetic measurements were made in May 2002. This paper briefly reviews previous attempts to geodetically measure surface deformation across the SWSZ, summarises the scientific rationale for the new project, describes the network design and observations used, reports on the results of the May 2002 campaign (epoch-one), and discusses future work, including issues pertaining to the likely amount of surface deformation that can be detected.

Keywords: intraplate deformation, geodesy, GPS, south-west seismic zone

Introduction

The Australian continent, which lies entirely within the Australian tectonic plate, is subject to reasonably significant intraplate seismic activity (Wdowinski 1998). In Western Australia, a near-linear belt of such activity extends in an approximately northwest-southeast direction across the south-western corner of the State (Fig 1), which Doyle (1971) termed the south-west seismic zone (SWSZ). The SWSZ is one of the most seismically active areas in Australia (*e.g.* Everingham & Tilbury 1972), with the notable 1968 Meckering (magnitude 6.9), 1970 Calingiri (5.7), 1979 Cadoux (6.0), and more recently the 2001 Burakin (5.1) and 2002 Burakin (5.2) earthquakes. Since the SWSZ lies as close as ~150 km to the ~1.4 million people living in the Perth region, it poses a distinct seismic hazard (*e.g.* Gaull & Michael-Leiba 1987).

Knowledge of contemporary deformation is potentially an important component in understanding the earthquake activity in the SWSZ. However, little is currently known about the magnitude and orientation of any deformation. All that is presently known is that the western half of Australia is currently subject to an east-west-directed compressional stress regime (Reynolds & Hillis 2000; Zobak 1992). The expected association of surface expressions of deformation with seismic activity, though the two are not necessarily interdependent (*e.g.* Jackson & McKenzie 1988), has led to the use of terrestrial geodetic monitoring in parts of the SWSZ (discussed later). However, the amount of deformation in the SWSZ, as inferred from seismic monitoring conducted over the last three decades by Geoscience Australia, GA (formerly the Australian Geological Survey Organisation, AGSO), may be as small as 0.5 mm per annum, thus presenting a significant challenge to geodetic monitoring techniques in the SWSZ (*e.g.* Featherstone 1998). If the surface deformation were less than the proposed 0.5 mmy^{-1}, then this would suggest that the recent seismicity is atypical at a geological time scale.

Intraplate seismic activity has only received serious scientific attention in recent decades (*e.g.* Wdowinski 1998; Gaull & Michael-Leiba 1987; Snay *et al.* 1994). Due to the infrequent nature of intraplate earthquakes and extended recurrence periods for very large earthquakes in these zones (*e.g.* Weber *et al.* 1998), the inevitable extrapolation of data collected over the last few decades introduces a great deal of uncertainty in their analysis. Therefore, there is the need for independent, yet complementary, estimates of the rates of deformation in addition to those inferred from seismology.

The most effective means of quantifying contemporary surface deformation at discrete points over large areas is through high-precision geodetic measurements. In a deforming region, the amount of deformation can be quantified using repeated measurements of position, angles, distances, or a combination of these among a network of stable ground points. Historically, the measurements were made using conventional terrestrial surveying techniques (*i.e.* triangulation by measurement of angles, trilateration by measurement of distances, or a combination of both). Now, measurements from the Global Positioning System (GPS) have taken over as the primary means with which to quantify regional deformation (*e.g.* Bevis *et al.* 1997; Bock *et al.* 1997; Clarke *et al.* 1998; Weber *et al.* 1998; Pan *et al.* 2001).

Due to the small amount of expected deformation in the SWSZ (if indeed there is any surface expression of it) and the low precision of the terrestrial and *ad-hoc* GPS measurement methods then used, previous studies have proved inconclusive. Therefore, a more rigorous approach is required. Accordingly, a 48-ground-point GPS-geodetic deformation monitoring network has been established across the SWSZ (Fig 1), for which epoch-one GPS-geodetic measurements were made during May 2002. This collaborative venture involves funding and scientists from GA (Minerals and Geohazards, and National Mapping Divisions), the Western Australian Department of Land Information (DLI), the New Zealand Institute of Geological and Nuclear Sciences (GNS), Curtin University of Technology, and the University of Western Australia. This paper summarises the scientific rationale for this joint venture, describes the permanent network of ground monuments, gives results of the May 2002 GPS campaign and discusses the future work, including issues pertaining to the likely amount of surface deformation that could be detected using the GPS techniques described.

Previous geodetic deformation estimation in the SWSZ

There have been several attempts to geodetically measure surface deformation in various parts of Australia. Wellman (1981) presented an analysis and interpretation of repeat geodetic survey data for monitoring horizontal surface deformation throughout south-east and south-west Australia. In part of the SWSZ, Wellman (1981) utilised results from a combination of first-order (Anon 2002) triangulation observations and resurvey trilateration observations. Note that the repeat survey used a different geodetic surveying technique than the initial survey, as well as different instrumentation.

Coleman & Lambeck (1983) seriously questioned the validity of Wellman's (1981) conclusions, arguing that the interpreted deformation is not significant because several critical factors were neglected. Clearly, this raises doubt as to the significance of any claimed crustal movement in the SWSZ, though admittedly Wellman (1981) states that 'it is irregular in magnitude and direction' in the SWSZ, which concurs with the later analysis performed by Featherstone (1998). Clearly, it is uncertain whether Wellman's (1981) estimates of horizontal surface deformation in the SWSZ are real or are simply an artefact of measurement, reduction and adjustment errors. This uncertainty is compounded by the inclusion of the same data in the least squares adjusted coordinates between measurement epochs (Coleman & Lambeck 1983).

Soon after the 1968 Meckering earthquake, DLI initiated a programme of episodic repeat-geodetic measurements to monitor surface deformation around the Meckering region, until 1995. This involved nine horizontal geodetic monitoring cells over parts of the SWSZ, and conducting second-order geodetic levelling over a large proportion of the SWSZ, which was used by Wellman & Tracey (1987). Changes in funding and advances in geodetic measurement technology dictated that the horizontal monitoring used both terrestrial-geodetic and GPS-geodetic techniques, which can exhibit scale differences (*cf* Savage *et al.* 1996). Featherstone (1998) analysed the horizontal DLI data and argued that these investigations of the SWSZ were also inconclusive (*cf* Coleman & Lambeck, 1983). Based on comparisons of the measured distances (*i.e.* the primary observations), no statistically significant changes were detected in relation to the expected precision of the measurement techniques used. Moreover, there were contradictory estimates of extension and compression for the same baselines. Although one of DLI's monitoring cells (to the west of Meckering) did show some significant differences, these could be simply attributed to instrumentation differences (Featherstone 1998).

In 2000, the first-named author reoccupied parts of this monitoring cell with Leica CRS1000 GPS receivers. Unfortunately, the GPS data collected were not of sufficient quality to resolve any motion. Nevertheless, the field survey was useful because it was discovered that several of the ground monuments were difficult to accurately centre over (*e.g.* 10 mm spikes set in concrete with no drill-hole; *cf* the monument to the right in Fig 2), and many of the monuments were not set on bedrock. At least one was demonstrably unstable, moving when kicked very gently. Therefore, the apparent statistically significant deformation observed in this area could simply be due to one or all of different GPS instruments, GPS-antenna centring errors over the ground marks, and disturbance of the marks between observation epochs.

From all these previous studies, there is clearly no consensus as to whether any surface deformation has actually been detected in the SWSZ, or whether observation and data reduction errors have been misinterpreted as deformation (*cf* Coleman & Lambeck 1983; Featherstone 1998). Accordingly, the consortium has taken a fresh approach to geodetic deformation monitoring in the SWSZ, as follows.

The new 48-point SWSZ network

The most effective means of quantifying contemporary surface deformation at discrete points over large areas by GPS is through a network of continuously operating geodetic GPS receivers. Such an approach has been adopted in tectonically active regions such as Southern

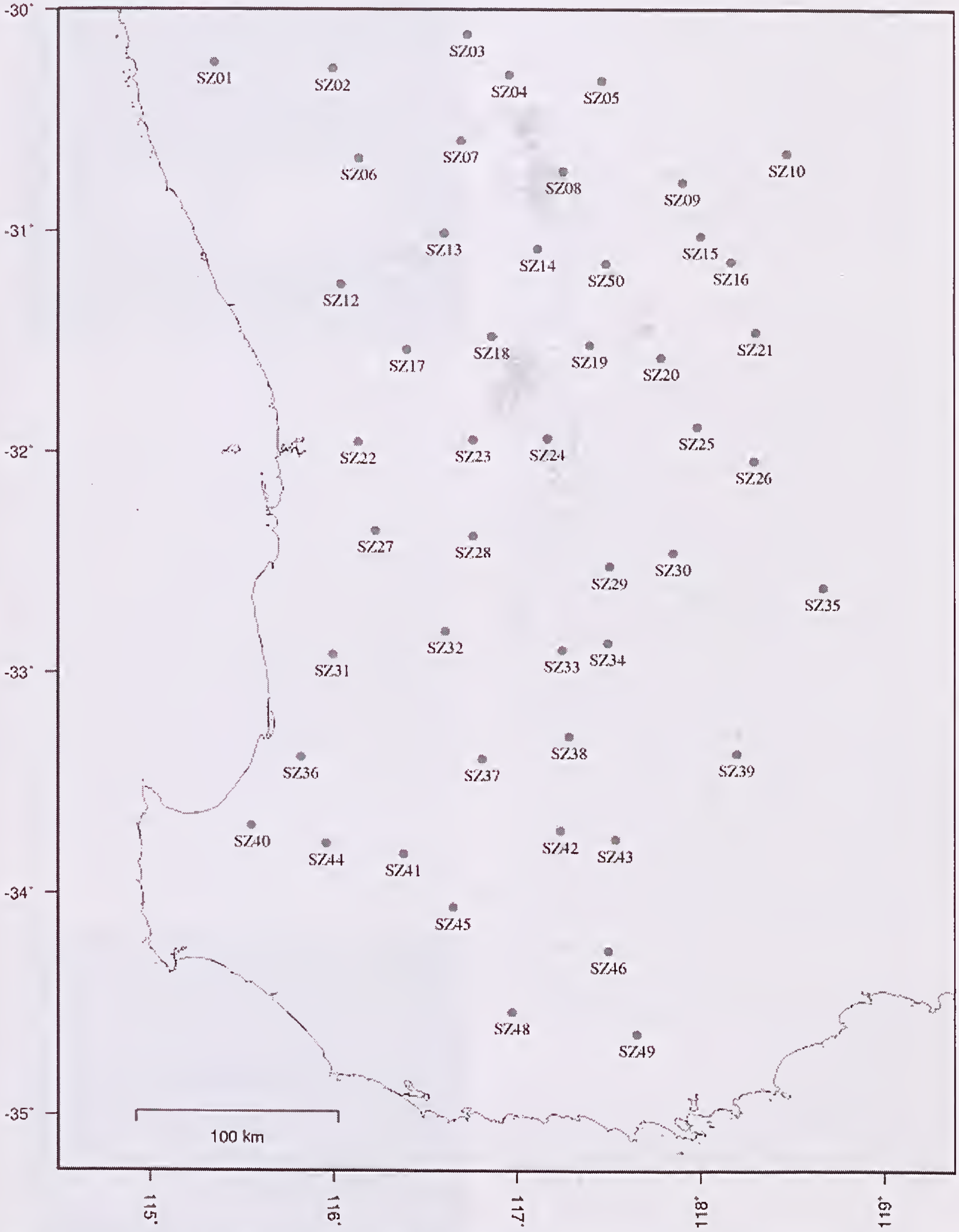

Figure 1. Distribution of the 48 GPS stations in the SWSZ, which were each surveyed for 5-7 days during May 2002 [SZ11 and SZ47 were not placed]. The dots show all the recorded earthquakes in this region (1970-2002).

California (*e.g.* Bock *et al.* 1997) to obtain continuous coordinate time-series for the points occupied, from which velocities can be computed and surface deformation inferred. However, this would be an extremely costly undertaking across the reasonably remote SWSZ, with each station costing up to approximately A$70000 to install. A more economically efficient compromise is to establish a network of permanent ground monuments installed rigidly on bedrock, coupled with episodic repeat GPS surveys collected over several days per station, as was used by, for example, Clarke *et al.* (1998) and Pan *et al.* (2001). This episodic monitoring approach has been adopted in the SWSZ.

Unlike conventional terrestrial surveying methods, modern geodetic-GPS also offers the opportunity to directly measure both the absolute (*i.e.* in a global reference frame) and relative (*i.e.* between points in the local region of interest) deformation of the ground monuments. However, the small amount of deformation expected in the SWSZ still poses a technical challenge to continuous, and more so the episodic, GPS deformation monitoring. Based on the inconclusive results of the previous geodetic surveys over an approximate 30-year time span, the most important consideration is to determine if the new GPS-geodetic time-series will give an accurate representation of actual surface deformation, not simply an artefact of errors associated with the measurement and data processing techniques. As such, it is necessary to eliminate systematic errors from the episodic GPS-geodetic monitoring network as practically and economically possible.

Early in 2002, a 48-point network of permanent ground monuments was established by the consortium (Fig 1). For each of the 48 sites, Geoscience Australia selected potential granite rock sites from digital geological maps. DLI then used these to select the final site location and installed near-ground-level forced-centring pillars in bedrock. These ground monuments (Fig 2) were set using three epoxy-resined bolts set in drill-holes in the bedrock with nuts to level the stainless steel baseplate with respect to the local vertical. Once level, the screws and baseplate were set in more epoxy resin and fast-setting concrete, respectively. A standard 5/8-inch (Whitworth) thread had previously been set in each baseplate for the GPS antennas, or other geodetic instruments, to be re-centred exactly during each episodic occupation. Reference marks were also set at ~120-degree intervals and at ~3 m surrounding each mark, so that if disturbed or destroyed, the primary mark can be relocated to millimetre-precision.

Between 30 April and 22 May 2002, approximately 20 sites were simultaneously surveyed near-continuously (except for equipment failures at a few sites) for between 5 and 7 days. Each site used forced-centred GPS antennas, oriented as closely as possible to north using shims [washers of different diameter], on the permanent ground marks (Fig 3). Dual-frequency code and carrier-phase data were logged at a 30-second interval from all GPS satellites above a 5-degree elevation angle. The geodetic GPS receivers used were Ashtech Z Surveyor and Z12, Trimble 5700 and Leica CRS1000. The GPS antennas used were Ashtech [Dorne-Margolin-type] choke-ring, Trimble Zephyr (Fig 2), and Leica [Dorne-Margolin-type] choke-ring (Fig 3). The Dorne-Margolin-type antennas reduce multipath (reflected GPS signals) by the geometry and depth of the choke-rings, and the Zephyr antennas use advanced signal processing to reduce multipath (see Dawson 2002). Cost considerations and equipment availability among the consortium members precluded the preferable use of the same models of GPS receivers and antennas.

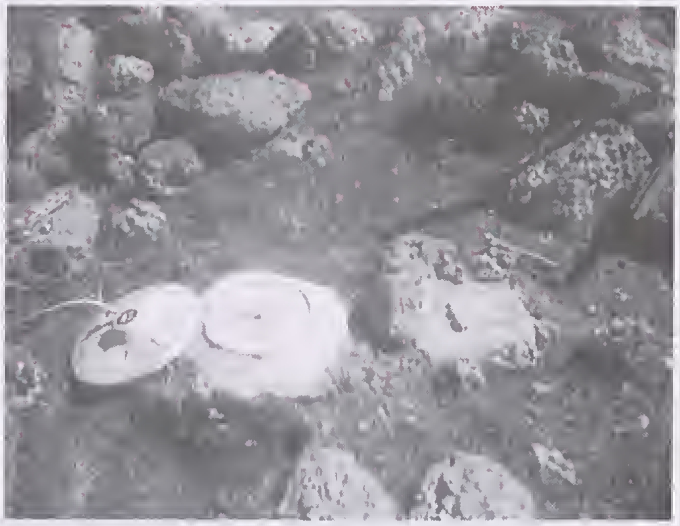

Figure 2. A newly installed ground monument (left); the ground mark to the right is part of the existing Western Australian geodetic network maintained by DLI.

Five Ashtech Micro Z GPS receivers and antennas were operated continuously for the entire campaign (at newly established ground marks SZ07, SZ15, SZ20, SZ33 and SZ48 (Fig 1)). This provided a "backbone" of stations in order to precisely link the surveys. The remaining sites were occupied in three near-one-week phases (*i.e.* approximately 20 simultaneous occupations including the five continuous sites) from north to south with three survey teams moving and maintaining around five stations each. The mobile survey teams would periodically check the receivers, which in some cases proved essential because of power failures. At least 5 days of near-continuous dual-frequency GPS data were obtained from all but two of the sites.

Figure 3. The GPS receiver was powered by a combination of solar panels and car batteries and left unattended (excepting checks) during each site occupation.

The 48-point GPS monitoring network will be used predominantly for monitoring horizontal deformation across the SWSZ, because GPS is inherently less precise in the vertical (shown later) due mainly to a combination of the geometry of the satellites (with them being only above the ground-based antennas) and inaccurately modelled atmospheric refraction of the GPS signals. Geodetic spirit levelling is the most precise means with which to monitor vertical deformation at discrete points. Therefore, if vertical deformation is sought over the SWSZ, it is probably best to reoccupy and extend the levelling network used by Wellman & Tracey (1988).

GPS Data Processing and Results

Any geodynamic deformation monitoring campaign that uses GPS (episodic or continuous) requires sophisticated data processing and error modelling. Firstly, geodetic quality (*i.e.* dual-frequency code and carrier-phase) instruments and antennas that reduce the effects of multipath must be used. Secondly, scientific GPS data processing software must be used. Commercial GPS data processing software is inadequate because of its approximated algorithms and inability to model the small, yet important, biases that would obscure the small, if any, surface deformations in the SWSZ.

The National Mapping Division of Geoscience Australia processed the GPS data collected for epoch one (Dawson 2002) using the Bernese version 4.2 GPS software (Hugentobler *et al.* 2001), closely following the procedures adopted by the regional analysis centres of the International GPS Service (IGS; http://igscb.jpl.nasa.gov/). This data processing included the rigorous modelling of systematic errors, including variable ionospheric and tropospheric signal refraction, periodic solid-Earth- and ocean-tide effects, and antenna phase-centre variations. The GPS satellite orbit information used was that provided in the final IGS orbital product, which was held fixed together with Earth-orientation parameters. Carrier-phase ambiguity resolution was attempted on all baselines for all GPS data collected above an elevation angle of 10 degrees.

Besides the GPS data collected in the SWSZ, GPS data were also collated from continuously operating GPS receivers at Alice Springs, Karratha, Ceduna and Perth, whose 30-second (dual-frequency code and carrier-phase) data are made freely available through the IGS. These were included since their data are processed daily by the IGS analysis centres and hence have extremely accurately (sub-cm) known coordinates in a global, dynamic, reference frame. When the position of a point is expressed in a dynamic reference frame, it is accompanied by the particular epoch to which it refers. This recognises the fact that the coordinates of the point will change due to global plate tectonic motion and hence the point also has an associated velocity (curiously, no mention is made of intraplate deformations in the models used). The estimates of coordinates and velocities for Alice Springs, Karratha, Ceduna and Perth are computed by the International Earth Rotation Service (IERS) using all available IGS GPS data and are updated approximately yearly in a solution termed the International Terrestrial Reference Frame (ITRF).

The latest realisation is ITRF2000 (http://lareg.ensg.ign.fr/ITRF/ITRF2000), which used all GPS and other space-based data up until the end of the year 2000 to compute the coordinates and velocity estimates for each point. Hence, including data from the IGS stations (with published ITRF2000 coordinates and associated velocities) in the GPS network solution has enabled the positions of the 48 SWSZ monitoring points to be computed relative to the four nearby IGS stations and to express their coordinates in the ITRF2000. The velocities of the 48 SWSZ monitoring points could then be subsequently computed from the coordinate estimates obtained at different epochs. For the epoch-one survey, the coordinates of the four IGS stations were fixed at their ITRF2000 values at the campaign mid-epoch 2002.37, therefore the coordinates of the SWSZ monitoring points also refer to ITRF2000 epoch 2002.37

While the GPS data were collected continuously at each monitoring point over the 5-7 day observation period (excepting the five stations that were occupied nearly continuously for 22 days), discrete three-dimensional position solutions were obtained using the data for each (Universal Time) day, which were then combined using the least squares techniques to obtain the final ITRF2000 epoch 2002.37 coordinate estimates (Dawson 2002). This approach enables some internally estimated quality assurance of the solution, via the computation of coordinate standard errors (1σ) from the variation of each daily solution from the mean. Importantly, such 1σ are only indicators of the internal precision of the solution, namely that there is a 68% probability that the position solution obtained from any given day will be equal to the mean value in each dimension. When these three dimensions are combined to form a horizontal ellipse or three-dimensional ellipsoid, the error magnitudes must be scaled for multivariate statistics (*e.g.* Anon. 1996).

Fig 4 and Table 1 summarise the internally estimated precision of the ITRF2000 (epoch 2002.37) coordinates of the 48 SWSZ stations. The geodetic coordinates (*i.e.* latitude, longitude and ellipsoidal height) are given by Dawson (2002). From Fig 4, 46 of the 48 occupied stations have an internally estimated precision of 1.5 mm in the horizontal [43 have a precision of 1 mm]; the vertical precision was generally better than 7 mm. Two stations (SZ23 and SZ36) gave very poor results due to Leica CRS1000 equipment failure (Fig 4). Therefore, Table 1 includes a summary of the results excluding these two outliers.

The internal precision estimates summarised in Table 1 and Fig 4 provide an indication of the consistency of

Table 1

Descriptive statistical summary of the internally estimated precision (1σ in mm) of the epoch-one GPS-derived coordinates (ITRF2000, epoch 2002.37) of the 48-point network across the SWSZ (values in parentheses exclude the two outliers at SZ23 and SZ36)

	1σ East	1σ North	1σ Vertical
Maximum	3.4 (1.4)	8.3 (1.5)	21.8 (8.8)
Minimum	0.6 (0.6)	0.7 (0.7)	3.5 (3.5)
Mean	1.09 (0.99)	1.36 (1.16)	6.80 (6.18)
STD	0.50 (0.16)	1.10 (0.17)	3.20 (1.06)

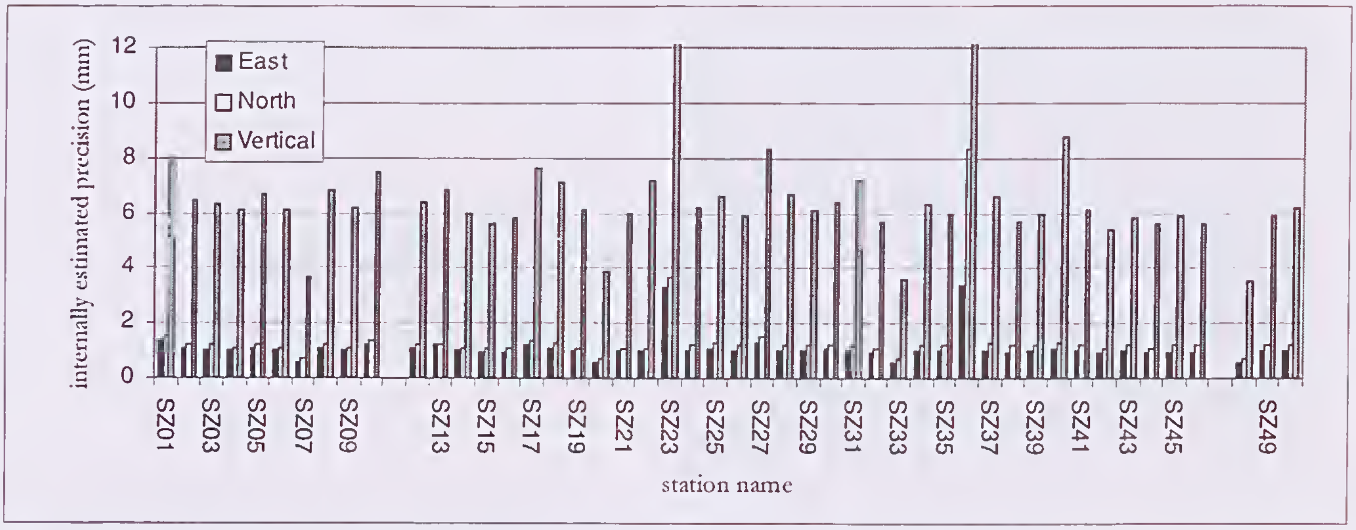

Figure 4. Internally estimated precision (1σ) of the epoch-one GPS-derived coordinates (ITRF2000 epoch 2002.37) of the 48-point network across the SWSZ (units in mm) [SZ11 and SZ47 were not placed]

the solution and suggest that the GPS data were generally of high quality and there were no major signal interference or reception problems. In addition, systematic error effects that vary may over the duration of the epoch-one campaign, such as atmospheric delays, were well mitigated by sophisticated modelling during the data processing. Nevertheless, the figures above are by no means an indication of coordinate accuracy. Inter-instrumental and site-dependent biases, notably unmodelled multipath, (*i.e.* systematic errors) will result in different coordinates being computed for the same station when surveyed with different GPS antennas and receivers.

For instance, the electrical phase centres of the antenna at which the GPS signals are received are not necessarily coincident with the physical/geometrical centre of the antenna due to mechanical imperfections, and also vary depending on the antenna make and model. Therefore, future surveys should endeavour to use the same receivers and antennas at the same ground marks. If not, great care will be exercised to account for the above-mentioned systematic errors so that any coordinate differences are not misinterpreted as surface motion in the SWSZ (cf. Lambeck & Coleman 1983; Featherstone 1998).

Discussion and Future Work

Monitoring results from previous studies of geodetic surface deformation of the SWSZ have proved inconclusive due to errors in the data collection and reduction techniques used. Therefore, a 48-point network of dedicated permanent ground monuments, with forced-centring apparatus, has been established to quantify any surface deformation associated with the seismic activity across the central part of the SWSZ with a view to long-term GPS-geodetic monitoring of their deformation. The consortium first occupied the epoch-one network during May 2002 using four different types of GPS receivers and antennas. Excluding two outlying stations (based on statistical analysis and problems encountered in the field), the internal precision estimates of the computed ITRF2000 (epoch 2002.37) horizontal coordinates show a mean precision of ~1 mm in north and east (and ~6 mm in the vertical). The vertical GPS coordinates will probably not be used because levelling is a more precise technique for detecting vertical motion.

Based on the accuracy with which the horizontal coordinates of the monitoring points can be estimated and the expected episodic reoccupation frequency of the monitoring epochs, indications of the time required to detect a particular magnitude of surface deformation can be estimated. Using the relationship provided by Coates *et al.* (1985), Dixon (1991) states that the uncertainty σ_v in any station velocity estimate is dependent on the single measurement point accuracy (not precision) σ_m, the (assumed constant) epoch separation Δt, and the time T between the first and last epoch:

$$\sigma_v = \frac{\sigma_m}{T}\left[\frac{12T/\Delta t}{(1+T/\Delta t)(2+T/\Delta t)}\right]^{1/2}$$

For a point measurement accuracy of 1.5 mm, an epoch separation (*i.e.* episodic re-measurement period) of two years and a total monitoring period of 10 years, this suggests a point velocity uncertainty of 0.2 mmy^{-1}. Extending the monitoring period to 20 years suggests a point velocity uncertainty of 0.1 mmy^{-1}. However, regarding the epoch-one results, it is stressed that, whilst the maximum horizontal internal precision estimate for the SWSZ monitoring points was ~1.5 mm (ignoring outliers), this is not an indicator of the accuracy of the point measurement and cannot necessarily be blindly used to obtain an estimate of the uncertainty in the computed velocity. Accordingly, the above velocity uncertainties are probably over-optimistic.

Furthermore, the equation for σ_v assumes negligible slowly varying systematic errors, yet coordinate time-series computed from the analysis of continuous GPS data by many analysts worldwide currently show pronounced seasonal variations (*e.g.* Dong *et al.* 2002). Blewitt *et al.* (2001) identified the response of the elastic solid-Earth to redistribution of surface load via seasonal changes in a GPS coordinate time-series. When surface deformation is monitored using coordinate time-series formed from episodic measurements, such seasonal effects could result in an under-sampled or aliased signal, resulting in biased velocity estimates. Hence in the presence of seasonal variations, simple linear regression techniques to estimate velocities (as above) may be inappropriate.

Another important consideration when computing station velocities is the correlation of the position error estimates between measurement epochs (*e.g.* Williams 2003). From an analysis of continuous GPS data, the resulting coordinate estimate each day, Mao *et al.* (1999) suggests that the velocity error may be underestimated by factors of 5-11 if such correlations are ignored. In the episodic approach to be used for the SWSZ network this is perhaps less critical, but nevertheless will be considered. When computing station velocities, the stability of the geodetic monument should also be assessed, namely that it remains firmly anchored in the ground and represents movement of the Earth's crust, not simply a local effect. This was addressed in the new SWSZ network as best as possible by only establishing sites on firm bedrock.

Forming coordinate time-series (and subsequently station velocity estimates) using GPS has the added complication that dynamic reference frames such as the ITRF are regularly updated, typically every 3-4 years. This becomes an issue for long-term episodic GPS deformation monitoring, since the precise satellite orbits attainable from the IGS are provided in the most recent realisation of the ITRF, which may be different from that used in the data processing of a previous GPS survey. In the data-processing approach adopted here, the estimated station coordinates are essentially in the same reference frame as the satellite orbit (as inferred via the control stations used). Since velocities can only be computed from coordinate estimates that are expressed in a common reference frame, it is usually necessary to re-process the data from a previous survey when the latest realisation of the ITRF becomes available, or transform the coordinates from the previous realisation of the ITRF to the most recent realisation (Boucher & Altamimi 1996). Therefore, these two different approaches will be experimented with after subsequent epochs are measured across the SWSZ.

The consortium intends to conduct a re-occupation of the 48-point network as soon as 2004. Depending on the number of different GPS receivers and antennas available, several reoccupations will be used to estimate inter-instrumental biases so as to better define the accuracy of the computed coordinates. However, where possible, the same GPS receivers and antennas will be used at the same stations as used for the epoch-one survey so that common systematic errors will cancel. Once reoccupations have been undertaken in 2004, and probably again in 2006, the GPS data will be reprocessed (using more sophisticated algorithms and techniques that may be available at that time, as well as implementing a consistent ITRF realisation) to give the first estimates of both absolute and relative station velocities in the SWSZ. These data can be analysed in a variety of ways, from simple vector plots through to stress and strain inversion (*e.g.* Wu *et al.*, 2001), in order to extract information relevant to Geoscience Australia's earthquake hazard research, as well as other programmes being undertaken by the consortium members.

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Distribution and Abundance of Benthic Macroalgae in the Swan-Canning Estuary, South-Western Australia

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Abstract

The macroalgal communities of the Swan-Canning Estuary were investigated between August 1995 and May 1997. Thirty-six macroalgal species were recorded, predominantly of the division Chlorophyta. Macroalgal species number was highest (15 to 22 species) in the lower, more marine reaches of the estuary, and in the seasons of hydrological change when freshwater flows were commencing or abating (*i.e.* spring and autumn). Macroalgal biomass was patchy both spatially and temporally: highest biomass was in the lower estuarine reaches (629 g.m^{-2} dwt), where mixed soft and hard substrata were present in spring (November 1996) after winter freshwater pulses had subsided. Macroalgal biomass was generally dominated by rhodophytes, especially the species *Gracilaria comosa*, although high biomass was also attributable to the phaeophyte *Cystoseira trinodis* at sites characterised by a hard substratum in the lower reaches of the estuary.

Keywords: Swan-Canning Estuary, benthic macroalgae, biomass, species number, *Gracilaria comosa*

(Manuscript received June 2003; accepted November 2003)

Introduction

The Swan-Canning Estuary is a large south-western Australian system that stretches more than 50 km inland from the coast at Fremantle. The system contains extensive areas of shallow sand-flats. Two rivers discharge into the system: the Swan-Avon River to the east, and the Canning River to the south, with catchment areas of approximately 119 000 km^2 and 20 000 km^2, respectively (Thurlow *et. al.* 1986). The suburban and industrial development of Perth city occupy a large proportion of the estuary's banks (Hodgkin 1987).

The Swan-Canning Estuary is a highly seasonal system, where the main influence is large freshwater pulses driven through the waterbody in winter. With the onset and dissipation of freshwater flows, the physico-chemical environment of the estuary changes. During winter (July to September), relatively high and sporadic rainfall events (over 100 mm per month) generate highly variable and pulsing river flows (>100 m^3.s^{-1}). Associated with the pulses are low salinities throughout most of the estuary (approximately 5 units at the surface although bottom waters near the mouth are up to 32 units), low temperatures (13–14 °C) and high light attenuation (Secchi disk depth 35 to 70% of the water column). The freshwater pulses lead to an elevation of nutrient concentrations; dissolved inorganic nitrogen concentrations are commonly between 0.6 and 1.65 mg.L^{-1} in fresher surface waters, and 0.15 to 1.25 mg.L^{-1} in the more marine bottom waters (Astill 2000). As rains and the freshwater input to the system subside, there is a gradual transition in the estuary's physico-chemical environment, largely brought about by marine waters penetrating into the estuary as a salt wedge, reaching some 55 km upstream from the estuary mouth by autumn (Astill 2000). At this time, salinity, temperature, and light penetration increase in all regions of the estuary (20 to 35, and 19 to 21 °C, 40 to 80%, respectively), and dissolved inorganic nitrogen concentrations decrease (<0.3 mg.L^{-1} throughout the system).

Macroalgae are a conspicuous biological component of the Swan-Canning Estuary. Allender (1981) recorded 29 species when he surveyed the estuary in the summer of 1968 between the junction of the Swan and Helena Rivers and the mouth of the estuary. Allender proposed that changes in the assemblages within the estuary could be spatially defined by the seasonal salinity regimes. Many of the species present were typical of eutrophic estuaries and have been recorded in the estuary since at least the 1970s (Allender 1981).

This study investigated the populations of attached and unattached macroalgae present in the Swan-Canning Estuary, almost thirty years after Allender's (1981) preliminary and qualitative investigations of this biological component of the Swan-Canning Estuary. The primary aims of this study were to investigate the macroalgal species now present in the system in comparison to Allender's findings, and to quantitatively describe the temporal and spatial variation within the macroalgal populations present in the estuary.

During the study, macroalgal assemblages were surveyed seasonally over two years (August 1995 to May 1997). Assemblages were investigated for a number of characteristics including species numbers, temporal presence and absence, and macroalgal biomass.

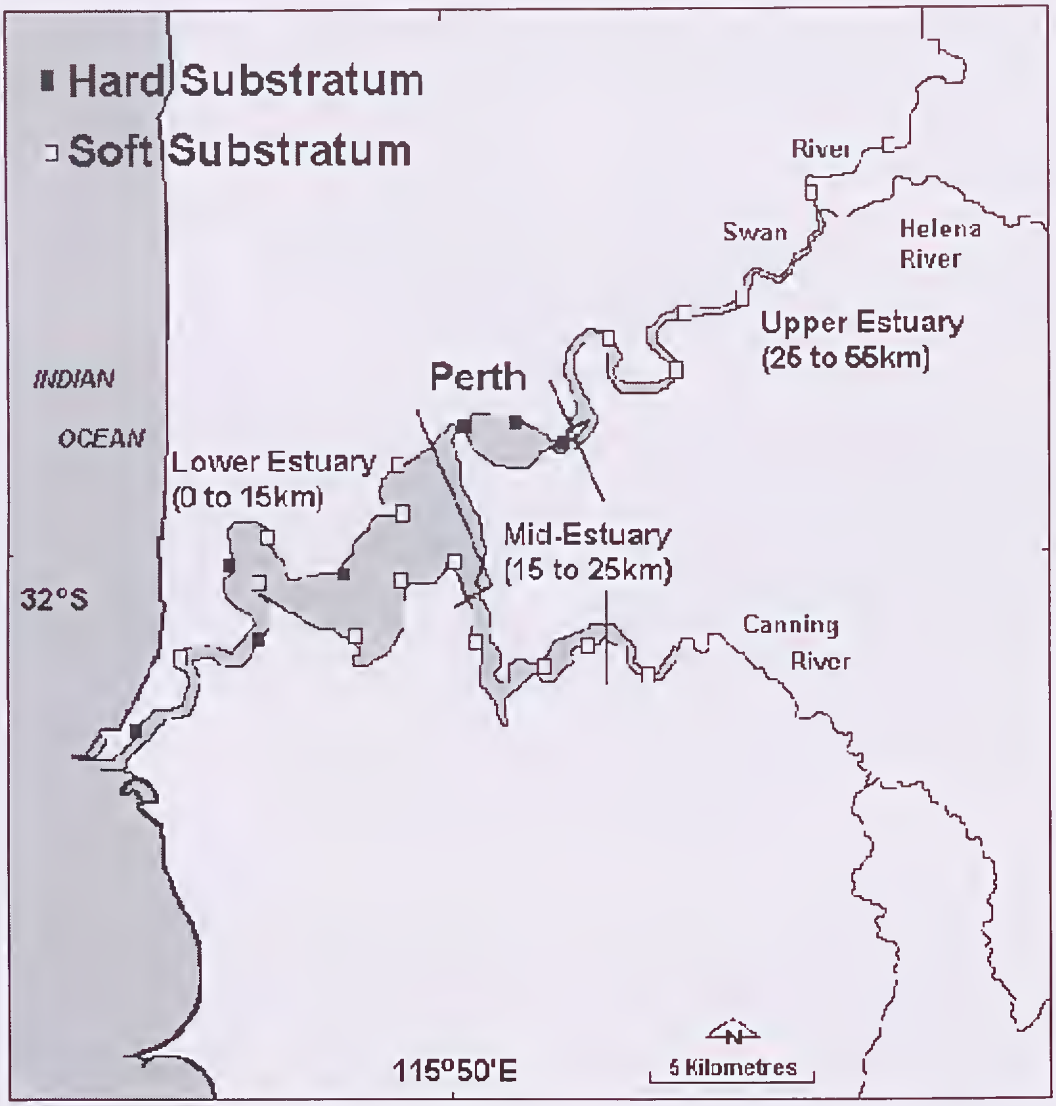

Figure 1. Location of macroalgal sampling sites (indicating hard or soft substrate), with estuarine region (lower, mid and upper) indicated, in the Swan-Canning Estuary

Materials and Methods

Macroalgal communities were sampled every three months between August 1995 and May 1997 at 28 sampling sites (Fig 1). The area of each site was approximately 50 m², and they were located near the banks of the estuary where water depths were less than 7 m. Sites were grouped into stratified regions of the system, and categorised as the 'lower reaches' (0 to 15 km upstream from the estuary mouth), the 'mid reaches' (15 to 25 km from the mouth), and the 'upper reaches' (25 to 55 km upstream).

At each site attached macroalgae were sampled using a 0.25 m² quadrat, within which all macroalgae were removed by hand. Unattached macroalgae were sampled using a 9.5 cm (id) perspex corer, which was pushed into the sediment over the benthic macroalgae and sealed. The macroalgae were then separated from the underlying sediment with a 2 mm sieve, and placed on ice. Five replicate samples were taken at each site (for both quadrats and cores); ten samples at sites where both attached and unattached macroalgae were present. Macroalgal samples were sorted into species, identified, then dried to a constant dry weight at 70–80 °C. Biomass estimates are means of 5 replicates, expressed as g dry weight.m^{-2} with associated standard errors. Salinity throughout this publication is referred to without units according to the Practical Salinity Scale. On this scale, salinity is defined as a ratio of conductivities and therefore cannot have units.

Analyses of Variance were performed using Statistica for the dependent variables species number and biomass. Post-hoc analyses were performed using the Tukey HSD test. All data were tested for normality and homogeneity of variance prior to analyses; data not normally distributed or with homogeneity of variances was log-transformed prior to analyses.

Results and Discussion

Macroalgal Species

A list of the macroalgal species recorded during the

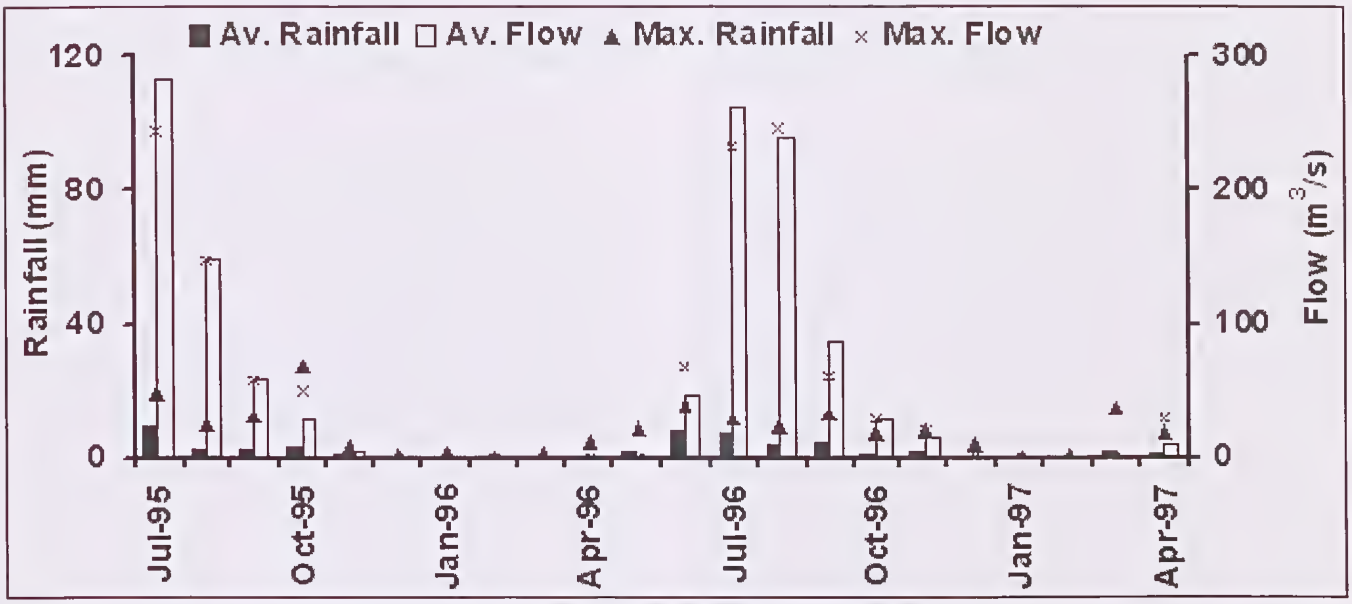

Figure 2. Average (Av.) and maximum (Max.) rainfall (in mm) and river flow (in $m^3.s^{-1}$) recorded for each month between July 1995 and April 1997

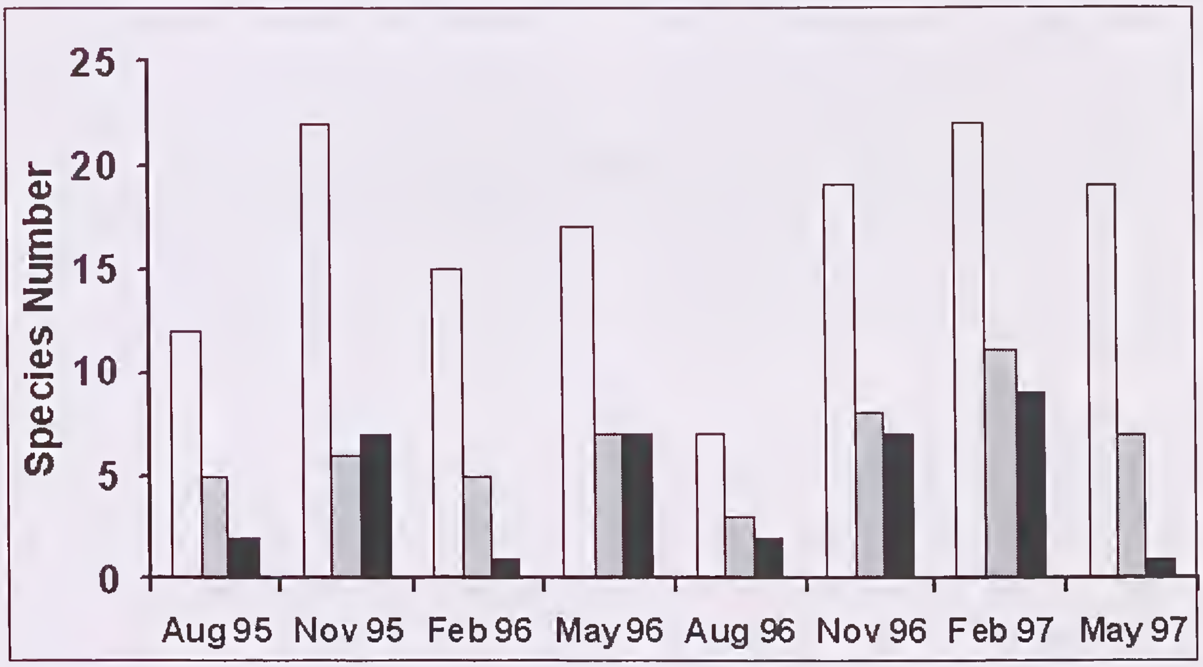

Figure 3. Macroalgal species number at sites within lower (☐; 0 to 15 km), mid (▨; 15 to 25 km) and upper (■; 25 to 55 km) estuarine reaches of the Swan-Canning Estuary

eight seasonal surveys is provided in Table 1, which includes the season in which each species was found. In total, 36 species of macroalgae were recorded during the study, dominated by chlorophytes (20 species) and rhodophytes (12 species). The highest total species number recorded in any one season was 20 in spring (November 1995) and the lowest was 6 recorded in winter (August 1996), the season of highest rainfall and river flows (Fig 2).

Regionally, the highest total species number was recorded in the lower estuarine reaches (Fig 3), where benthic salinities were over 30 in number in all seasons and macroalgal assemblages were dominated by species common to the nearby marine environment (Huisman 2000). Within this estuarine region, species numbers varied between 15 and 22 in spring, summer, and autumn, falling to between 7 and 12 in winter. The total species number was significantly lower in mid- and upper-estuarine reaches (Tables 2 and 3). In total, between 6 and 11 species were found in the mid-estuarine regions of the estuary in all seasons except winter (3–5 species), while in the upper reaches 7 to 9 species were recorded, although lower numbers of 1 to 2 species were found in winter. An exception to this generally low species number in the upper estuarine reaches was in November 1996 when 7 species were found in this estuarine region.

The total number of macroalgal species found during these surveys was 36, with the highest number recorded in any one season (spring) being 20 (Tables 2 and 3). These species numbers indicate a relatively diverse macroalgal community compared to other south-western Australian estuaries. For example, Hillman *et al.* (2000) listed only 13 macroalgal species from multiple surveys of the Leschenault Inlet between 1984 and 1993. The Leschenault Inlet also receives freshwater input from two rivers, the Collie and Preston Rivers, with an artificial connection to the ocean. Since construction of the Wellington Dam on the Collie River, freshwater input to the system has been significantly reduced, causing salinities within the Inlet to be marine throughout most of the year, and hypersaline in the northern end of the system. As reported here for the Swan-Canning System, the macroalgal assemblages in Leschenault Inlet were co-dominated by rhodophytes and chlorophytes, with the predominant species being *Gracilaria* sp and *Chaetomorpha linum*, respectively. Similarly, Lukatelich *et al.* (1984) recorded 8 macroalgal species in Wilson Inlet, primarily chlorophytes. In contrast, Phillips & Lavery (1997) found 40 macroalgal species in Waychinicup Estuary, dominated by phaeophytes and rhodophytes. Waychinicup Estuary is a small system (1.3 km in length) that has a strong tidal influence with a small, but consistent freshwater input. These hydrodynamic characteristics result in both vertical and horizontal variations in salinity within the estuary, with surface salinities at the head of the estuary as low as 22, and salinities at the mouth of the estuary effectively marine (34). As found in the current survey of the Swan-Canning Estuary, it was also in the lower reaches of Waychinicup Estuary, where extensive hard substratum is present, that most of opportunistic macroalgal species recorded during the investigation were recorded.

Allender (1981) first reviewed the macroalgal species of the Swan-Canning Estuary in 1968 over a one-year period. Allender surveyed benthic macroalgal communities present in the photic zone within the lower 25 km of the system. In total, he recorded 29 species comprising 11 chlorophytes and 14 rhodophytes, the majority of which he recognised as marine. As such, he proposed that the distribution of macroalgae along the horizontal axis of the estuary was strongly affected by the penetration of marine waters and the physiological tolerance of these species to freshwater inflows during winter. Accordingly, he found that the maximum horizontal distribution of species was during summer and the minimum was during winter. Allender (1981) proposed that macroalgal species in the Swan-Canning Estuary could be categorised as either annuals or perennials, depending upon whether the plants survived the winter season, and concluded that seasonal and temporal patterns in macroalgal communities of the system were largely due to the penetration and duration of marine waters into the estuary.

The present study provided preliminary identification of spatial and temporal patterns present in the macroalgal assemblages of the Swan-Canning Estuary, evidenced by the presence and absence of individual species according to season and estuarine region. In particular, highest species numbers were encountered in summer and autumn in the lower estuarine region, areas and times of high salinity and hard limestone substrate. Outside of these seasons and region, the number of macroalgal species was far fewer, mostly unattached macroalgae growing over soft sediments dominated by the species *Gracilaria comosa*.

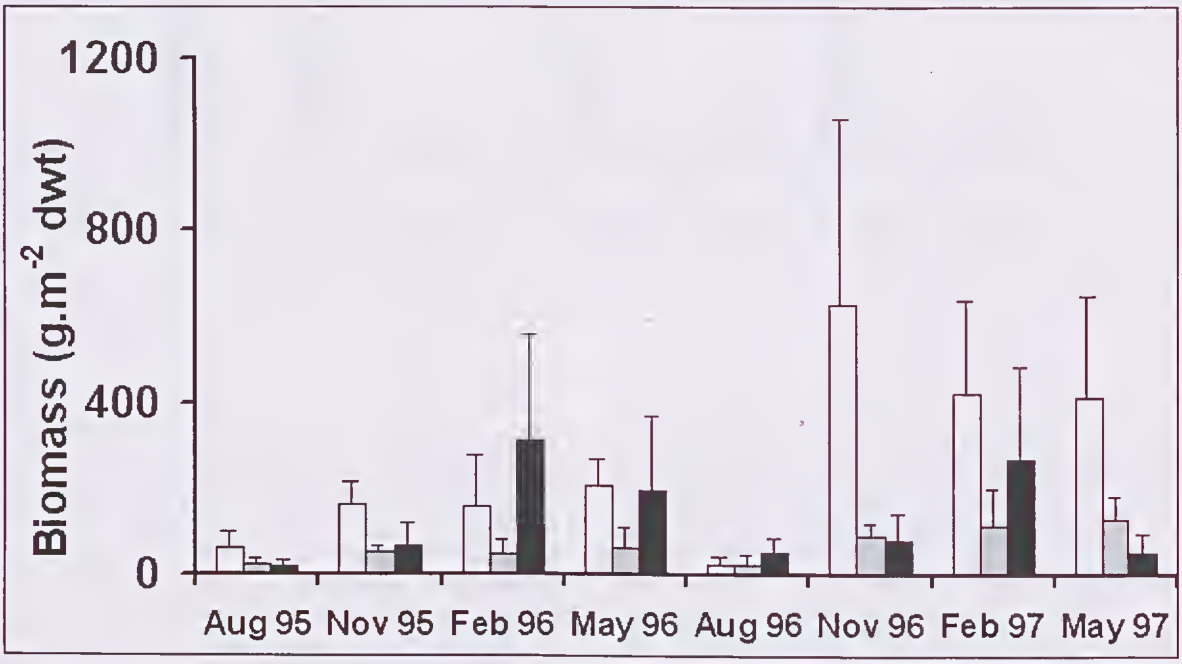

Figure 4. Macroalgal species number at (a) hard and (b) soft substrate sites within lower (□; 0 to 15 km), mid (▨; 15 to 25 km) and upper (■; 25 to 55 km) estuarine reaches of the Swan-Canning Estuary

G. comosa was found in all surveyed regions of the system on all sampling occasions, indicating that this species is euryhaline, tolerating osmotic change resulting from the advent of winter freshwater pulses. However, given that the species forms large unattached accumulations, the physical force of freshwater pulses results in the removal of *G. comosa* accumulations and therefore the disappearance of this species from many areas of the system during winter (Astill & Lavery 2001). Therefore, in addition to any physiological influence that freshwater pulses have on invasive marine species colonising lower estuarine reaches, such freshwater pulses have a physical influence on unattached species in the mid- and upper-estuarine reaches. Thus, it appears that the advent of freshwater pulses to the system in winter has a considerable effect, both physiological and physical, on benthic macroalgal assemblages throughout the estuary.

Macroalgal Biomass

The distribution and quantity of macroalgal biomass in the estuary was very patchy (Fig 4). Mean macroalgal biomass ranged between 18 and 629 g.m^{-2} dwt, varying according to estuarine region and season. Regionally, the highest mean biomass (629 g.m^{-2} dwt) was in the lower estuarine reaches, the combined result of *Cystoseira trinodis* stands and *Gracilaria comosa* accumulations. Mean macroalgal biomass in the mid- and upper-reaches was highly variable, ranging between 24 - 130 g/m^{2} dwt and 18 - 314 g.m^{-2} dwt, respectively. Seasonally, the highest mean biomass during the survey, 629 g.m^{-2} dwt, was in spring, and the lowest (18 g.m^{-2} dwt) was in winter.

Macroalgal biomass was generally dominated by rhodophytes, although macroalgae of the division Chlorophyta dominated at times in mid- and upper-

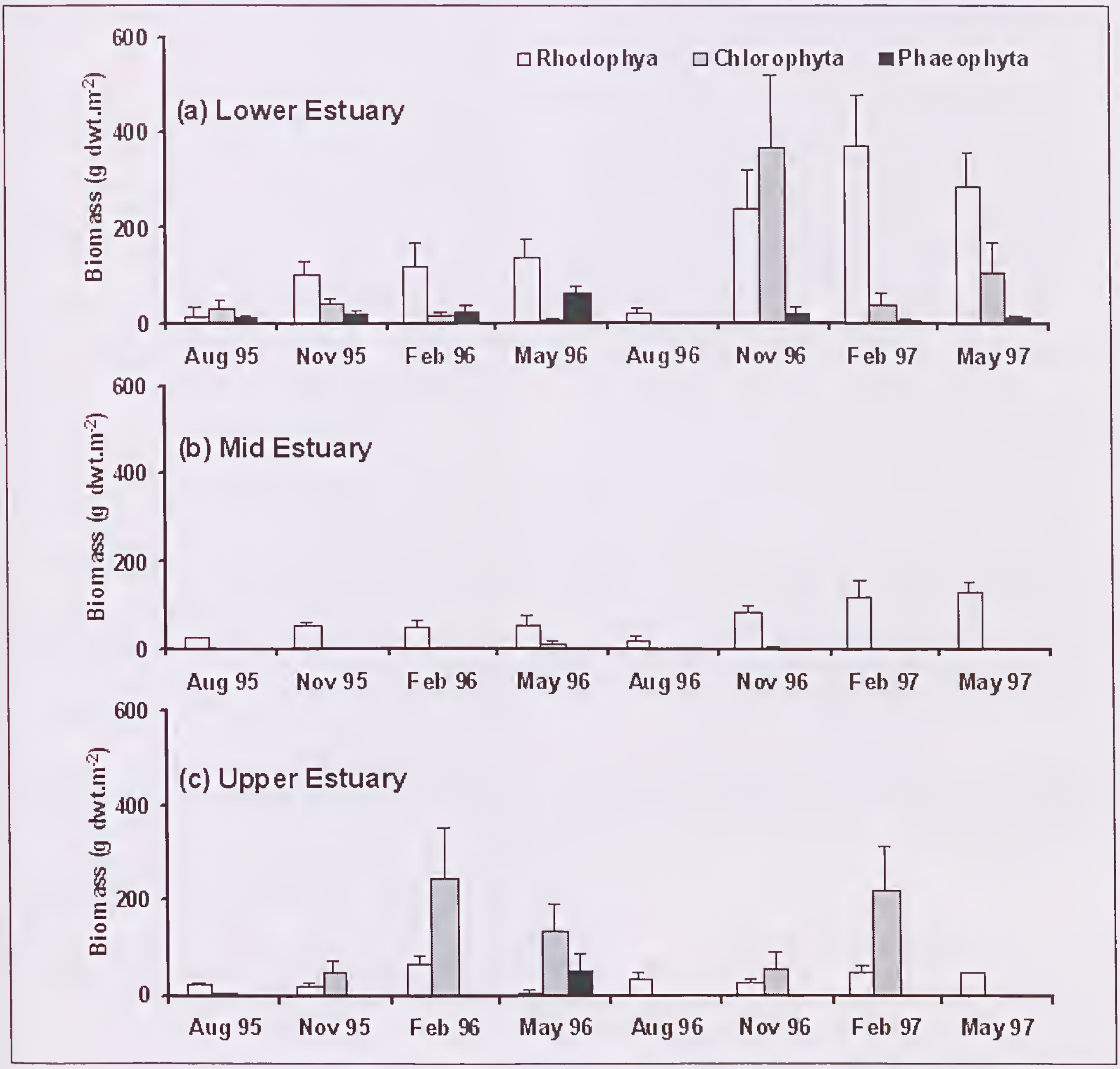

Figure 5 Mean macroalgal biomass at sites within lower (☐; 0 to 15 km), mid (▨; 15 to 25 km) and upper (■; 25 to 55 km) estuarine reaches of the Swan-Canning Estuary (± SE)

estuarine reaches (Fig 5). A large proportion of the macroalgal biomass was attributable to *Gracilaria comosa*. In winter, this species constituted over 90% of the total macroalgal biomass at the sampling sites, especially at those lacking hard substrate (*i.e.* predominantly mid- and upper-estuarine reaches). At freshwater-dominated sites in the upper region, a loose-rubble substratum was present and macroalgal biomass at these sites was dominated by the freshwater chlorophyte, *Chara* sp.

Biomass measurements in Leschenault Inlet showed a similar seasonal variation in macroalgal biomass, varying between 46 g/m^2 dwt in autumn/winter to 209 g/m^2 dwt in spring (Hillman *et al.* 2000). Macroalgal biomass in the Leschenault Inlet was dominated by chlorophyte and rhodophyte species (11 to 43% of total biomass, and 20 to 30% during spring, respectively). Similarly, in Peel Inlet, minimum and maximum macroalgal biomasses of 25 g/m^2 dwt (November 1988) and 237 g/m^2 dwt (April 1993) were recorded, although this biomass was predominantly (>85%) composed of chlorophyte species (Hillman *et al.* 2000).

Previous studies have attributed seasonal variability in macroalgal biomass to factors such as changes in light and nutrient availability (Kinney & Roman 1998; Collado-Vides 1994; King & Schramm 1976), while studies on drift macroalgae attribute a proportion of seasonal variation in biomass to water movement (Talbot *et al.* 1990; Virnstein & Carbonara 1985). Bell & Hall (1997) found drift macroalgal biomass in Tampa Bay (USA) to vary between almost nothing to more than 150 g/m^2 dwt. They suggested that variations in macroalgal biomass and distribution were related to local hydrodynamic regimes, such as wave action, currents, wind and tides.

In this study, *G. comosa* was commonly found in large, unattached accumulations overlying soft sediment, dominating macroalgal biomass in the system. However, this species was noticeably reduced or absent with the onset of winter freshwater flows, resulting in subsequent reductions in total macroalgal biomass throughout the system. From these observations it is proposed that seasonal freshwater flows in the system strongly affect the presence/absence of unattached macroalgal species through both physical and physiological means, and the quantity of macroalgal biomass present. Winter freshwater flows appear to be a dominant environmental factor controlling the presence, diversity and abundance of macroalgal assemblages in the Swan-Canning Estuary.

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The occurrence and impact of *Phytophthora cinnamomi* in the central-western Avon Wheatbelt bioregion of Western Australia

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Abstract

Dieback, the expression of the disease caused by *Phytophthora cinnamomi* Rands, has been little studied in the lower rainfall areas of the South-West botanical province of Western Australia. Our survey of access routes within the Department of Conservation and Land Management's Narrogin operational district (in the central-western Avon Wheatbelt bioregion) identified four areas with dieback infestations from 21 state forest blocks (forming Dryandra Woodland), 11 nature reserves and one private property block. All infestations were restricted to water-gaining sites lower in the landscape or those that had been subject to high disturbance. Fifty soil and root tissue samples were taken, with 5 returning positive for *Phytophthora cinnamomi*. Eleven plant species were observed to be dead or dying in association with the infestation sites. *Banksia* spp and other deep-rooted species are recommended for soil and root tissue sampling in this region due to their deeper root systems being more likely to support the survival of *P. cinnamomi* in the drier months. To avoid the spread of *P. cinnamomi*, it is recommended that under moist soil conditions vehicles should be clean on entry to nature reserves and State Forest blocks, road maintenance works should not move soil from gullies, and that vehicle access tracks across boggy crossings should be avoided or built to provide a hard, all weather running surface.

Key words: *Phytophthora cinnamomi* dieback disease, Narrogin, Avon Wheatbelt, management.

Introduction

A soil borne pathogen, *Phytophthora cinnamomi* Rands is a significant threat to the native vegetation of Western Australia, with infestation resulting in the deaths of susceptible plant species and altering the ecology of plant communities (Shearer 1994). Now widespread in the higher rainfall areas of the South-West of Western Australia, *P. cinnamomi* is having a major impact on the ecology of the jarrah forest (*Eucalyptus marginata* Donn ex. Smith) (Shearer & Tippett 1989) and other vegetation communities of the South-West botanical province (Shearer 1994).

While there are a number of studies have examined dieback (the expression of the disease caused by *P. cinnamomi*) in the jarrah forest (Shea *et al.* 1983; Shearer & Tippett 1989; Shearer & Dillon 1995), little work has been done on the impact and distribution of the disease in the lower rainfall areas of the South West botanical province. Shearer & Tippett (1989) considered that rainfall distribution is partly responsible for the decreasing incidence of *P. cinnamomi* with distance east from the Darling Scarp (decreasing in rainfall with distance east).

This paper discusses the results of a broad scale survey of the distribution of dieback in the central-

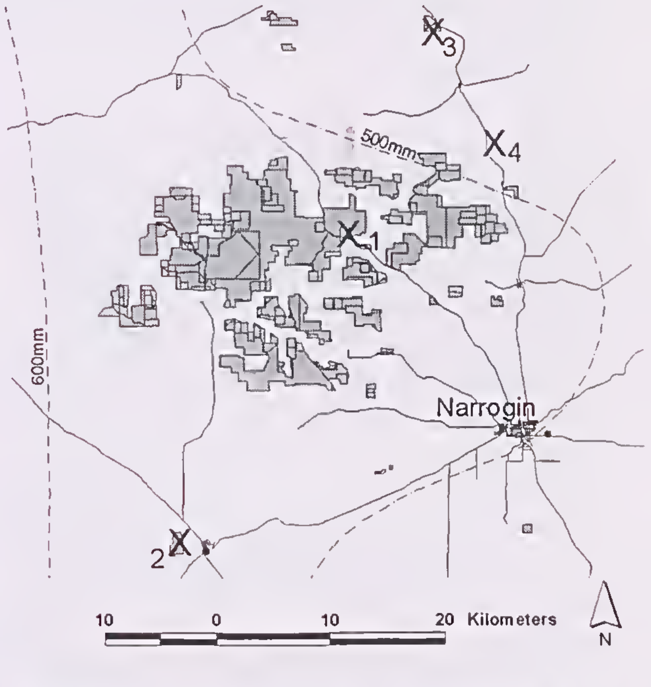

Figure 1. Location of the study area and infestations located in the central-western Avon-Wheatbelt bioregion of Western Australia. Shaded areas are State Forest or Nature Reserves; the dashed line is the maximum rainfall isohyet for Western Australia; crosses with numbers refer to site numbers from Table 1.

western Avon Wheatbelt bioregion covering the Department of Conservation and Land Management's (CALM) Narrogin operational district, approximately east of the 600 mm rainfall isohyet on the Darling Plateau (Fig 1). The area contains a number of nature reserves and the system of State Forest blocks that make up the Dryandra State Forest This work was undertaken to identify *P. cinnamomi* disease infestations and limit the risk of disease spread within the district. The impact of the disease and the species affected is also discussed.

Materials and Methods

Linear survey method

Due to the large size of the study area the 'linear survey' method (Anon 2001) was used to detect the disease symptoms caused by *Phytophthora cinnamomi* infestations. This involved slowly driving (less than 25 kmh^{-1}) or walking all accessible tracks within the forest block or nature reserve being considered, including boundary tracks along private property. Areas were mapped according their 'interpretability' for 25 m either side of the track. This technique is based on the premis that as an introduced pathogen, occurrence will generally be related to past disturbance or access routes. 'Interpretable' areas are those that have susceptible species in sufficient numbers to indicate whether the presence of *P. cinnamomi* can be adequately assessed (Anon 2001). 'Uninterpretable' areas are those where susceptible species are absent or too few in number to determine to the presence or absence of the disease. The boundaries of categories were marked using a handheld global positioning system unit (Garmin II plus). Sites with likely disease symptoms were examined on foot and a soil and root sample taken from dead or dying plants to confirm the presence of *P. cinnamomi.*

Soil and root samples

Fifty soil and root samples were taken from dead or dying susceptible plants, to a minimum depth of 30 cm (sterilised surface root samples were not taken). Samples were taken during April 2000 to May 2002. Axes and shovels were used to remove sections of root material and collect soil. All equipment used to collect the samples was sterilised before and after sampling with Methylated Spirits (95% v/v ethanol).

Sample baiting followed Marks & Kassaby (1974) where *Eucalytpus sieberi* F Muell cotyledons were used to determine whether the soil and root tissue samples were infested with *P. cinnamomi.* All samples were processed by the Vegetation Health service at CALM.

Infestation assessment

The impact at the *P. cinnamomi* infestations was assessed by determining the percentage of susceptible species that were dead or dying (see Anon 2001 for a list of susceptible species). Low impact refers to sites with few deaths; medium impact refers to scattered or <30% susceptible species deaths; high impact refers to sites with most susceptible species deaths (follows Shearer *et al.* 1997). At the Lol Gray infestation (Table 1, site 1) this was quantified using 10 x 10 m quadrats.

Voucher specimens were collected from dead and dying susceptible plant species at the Lol Gray infestation site. All specimens were submitted to the Western Australian Herbarium for incorporation into the collection.

Results

Infestations

Out of the 21 Dryandra Woodland blocks, 11 nature reserves and one private property, four dieback infestations were located (Fig. 1). All infestations were located on water-gaining sites (*i.e.* along a water course, drain or near a dam) or where there had been high disturbance in areas that were also low in the landscape. The infestation at Lol Gray State Forest in Dryandra Woodland was the largest at 16.4 ha (including a 10 m buffer). Three of the four infestations had low disease impact, while the Lol Gray State Forest, had low to high impact sites.

Susceptible species

Eleven susceptible plant species were recorded as dead or dying in association with the dieback infestations (Table 2). Other possible causes of death may include drought, roadside compaction of roots, or a combination of factors. These causes cannot be ruled out as a contributing factor in the deaths of species listed in Table 2. All are from plant families previously recorded as having species susceptible to dieback disease (Shearer & Dillon 1995) although six species are new to the *Phytophthora cinnamomi* dieback disease indicator species list (Anon 2001).

Table 1

Topograhical situation, soils/geology and disease impact for *Phytopthora cinnamomi* infestation locations.

Location	Topographical situation	Soils/ geology	Impact*
1. Lol Gray State Forest (Dryandra Woodland)	Lower slope beside drainage line and dam	Over granite	Low to High
2. Culbin Nature Reserve	Flat	Grey sand	Low
3. Hotham River Nature Reserve (8291)	Lower slope beside river	Grey sand	Low
4. Hotham River (private property)	Lower slope beside river	Grey sand	Low

* Low impact refers to sites with few deaths; medium impact refers to scattered or <30% susceptible species deaths; high impact refers to sites with most susceptible species deaths (follows Shearer *et al.* 1997).

Table 2

Susceptible species observed dead or dying in association with *Phytophthora cinnamomi* infestations in the Narrogin district.

Species	Family	Voucher No.	Site Impact +	% *
Allocasuarina ?huegeliana	Casuarinaceae	-	High	100%
Banksia cuneata #	Proteaceae	-	-	-
Banksia prionotes #	Proteaceae	-	Low to medium	-
Dampiera lindleyi	Goodeniaceae	LWS 1-9	Low	11%
Gastrolobium calycinum	Papilionaceae	LWS 1-8	Low to high	25- 90%
Hakea incrassata	Proteaceae	LWS 1-6	High	25%
Persoonia quinquenervis	Proteaceae	LWS 1-7	High	14%
Petrophile serruiae	Proteaceae	LWS 1-2	High	100%
Synaphea aff. *petiolaris*	Proteaceae	LWS 1-1	High	83%
Xanthorrhoea drummondii #	Xanthorrhoeaceae	LWS 1-3	Low to high	50%
Xanthorrhoea preissii	Xanthorrhoeaceae	-	Low	-

+ Low impact refers to sites with few deaths; medium impact refers to scattered or <30% susceptible species deaths; high impact refers to sites with most susceptible species deaths (follows Shearer *et al.* 1997). # returned a positive sample for *Phytophthora cinnamomi* when soil and root tissue samples were taken from around the base of plants at suspected infestations. Nomenclature follows Paczkowska & Chapman (2000). * within 10 m x 10 m quadrats.

% refers to dead and dying plants

Samples

P. cinnamomi was recovered from five of the 50 soil and root tissue samples taken from dead or dying plants across the study area,. The infestation at Hotham River (Table 1, site 4) had previously been identified from samples taken along the Pingelly to Narrogin highway (Shearer 1994).

Discussion

Shearer (1990, 1994) found that *Phytophthora cinnamomi* dieback disease impact is low in inland woodlands and shrub lands due to the low rainfall. Three of the four infestations located in our study area supported this finding. However we found that the level of impact in low rainfall areas can also be high, as observed at the Lol Gray infestation. At this site, a contributing factor may the granite outcropping (Table 1). Granite outcrops promote moisture runoff after rainfall or fog events (York Main 1997) and possibly there is some under-surface moisture accumulation; moisture is a key factor in the biology of the disease (Shearer & Tippett 1989). This effect may be comparable to the effect of concreted duricrust layers of the jarrah (*Eucalyptus marginata* Donn ex Sm.) forest where zoospores are transmitted laterally over the layer (Shea *et al.* 1983).

No infestations were observed away from low land and/or water-gaining or highly disturbed sites (Table 1). In this bioregion it is unlikely that there is sufficient moisture throughout the year to sustain an upland *P. cinnamomi* infestation. Kuhlman (1964) found that *P. cinnamomi* was unable to survive in dry soils. When screening for *P. cinnamomi* we therefore recommend taking soil and root tissue samples from deep-rooted plants such as *Banksia* spp. Moisture in roots and soil is likely to be higher deeper in the soil profile.

Management recommendations

1. In winter and spring or under moist soil conditions (where clumps of soil may attach that may carry propagules) vehicles should be cleaned down on entry into reserves and State Forest blocks to remove soil and root material underneath.
2. Road maintenance activities should avoid relocating soil from gullies and water-gaining sites.
3. Vehicle access tracks that cross gullies or areas of muddy sticky soils should be constructed to allow natural drainage. Track running surfaces should remain hard and not conductive to soil adhering to vehicles.

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Vegetation and flora of a diverse upland remnant of the Western Australian wheatbelt (Nature Reserve A21064).

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Abstract

In the Western Australian wheatbelt, small intact remnants of bushland can contribute significantly to overall biodiversity. Our comprehensive vascular flora survey of Nature Reserve A21064, a reserve of 110 hectares near the town of Arthur River, has highlighted this aspect. Comprehensive surveys of selective wheatbelt reserves provide benchmarks to help us better understand the flora and vegetation in this highly cleared and fragmented agricultural landscape. In the diverse flora of this relatively undisturbed upland remnant ten distinct plant communities encompassing heaths, herbfields, mallee and woodlands can be recognised. The survey identified 323 vascular plant taxa including one rare species, seven priority species and a number of taxa of special interest recorded from 51 families. Weeds accounted for 22 species (6.8% of total flora), however, the extent of invasion is relatively low.

Keywords: Vegetation and flora survey, upland remnant, biodiversity, wheatbelt woodlands

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Introduction

Nature Reserve A21064 is an upland bush remnant of high conservation value (*i.e.* "A" class nature reserve) with a diverse flora (see species list in Appendix 1). It is approximately 110 ha in area and is located about 190 km directly south-east of Perth near the town of Arthur River, Western Australia (Fig 1). The district has a dry Mediterranean type climate with very warm, dry summers and cool, wet winters. Average annual rainfall for the reserve is about 470 mm, which is typical of the wetter western (inner) margins of the wheatbelt.

The reserve is situated at the end of an eroded and generally flattened ridgeline and its upper slopes; the ridge is the watershed between Mailling Gully to the south and a smaller unnamed tributary to the north. These streams eventually drain into the Arthur River about 7 km west of the reserve. The Arthur River and adjacent Norcott Plains also run north of the reserve, about 3 km away. The reserve is a small L-shaped remnant with the longest east-west boundary (1.9 km) roughly parallel to the ridgeline/plateau. The north-south arm of the L measures approximately 1.2 km (Fig 2). Slopes descend gently off the ridgeline and the predominant aspect is north or north-west. A pattern of low undulating hills/ridges with interspersed small valleys and/or plains is typical locally and is a familiar topography for much of this inner wheatbelt region. Granite outcrops and/or lateritic breakaways are often found on the upper slopes or hilltops. Historically, many upland areas were not cleared for cropping because of the rougher topography. Also upland areas were generally abundant in the poisonous *Gastrolobium* species that killed domestic stock. Alternatively, some were left as 'shade and shelter belts'. Today, very few of these upland remnants have survived completely intact. Significant numbers have had a reduction in tree cover due to past logging (*e.g.* for timber and fence posts), insect pests, disease *etc*, and this has occurred in a

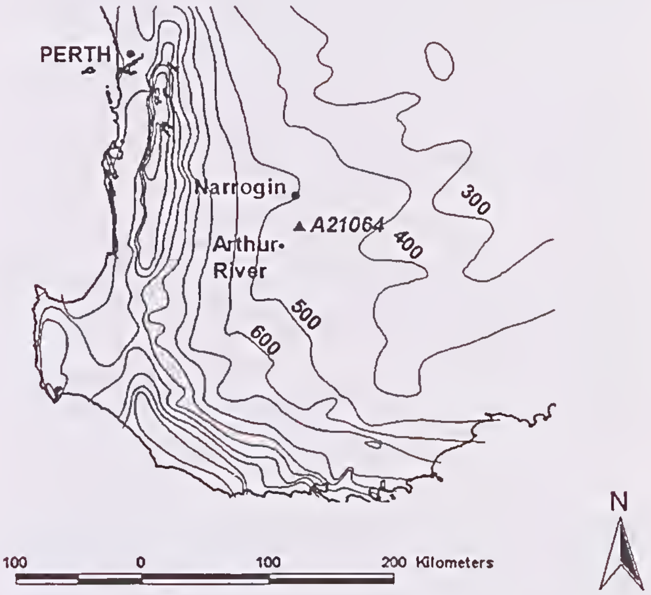

Figure 1. Location of A21064 Nature Reserve, near Arthur River, in the south-west of Western Australia; also shown are 100 mm rainfall isohyets.

relatively short time frame (Landsberg *et al.* 1990). The majority of these remnants are also depauperate in understorey taxa due to selective clearing (*e.g.* of 'poison plants'), frequent grazing by domestic stock, changed burning regimes, nutrient enrichment, weed invasion, and other human influenced disturbances (Hobbs & Atkins 1988; Hobbs 1993; Panetta & Hopkins 1991; Pigott 1994; Yates & Hobbs 1997; Yates *et al.* 1999; Yates *et al.* 2000).

The wheatbelt region as a whole has been altered from a mosaic of perennial native vegetation to predominantly cleared agricultural land with fragmented small bushland remnants (Hobbs 1998; Scanlan *et al.* 1992). A21064, which is surrounded by agricultural land, is no different. Beard (1980a) mapped the pre-existing vegetation cover of this entire region using aerial photography in conjunction with a wide-ranging examination of the remaining bushland remnants and their preferred habitat requirements (*i.e.* soil, slope, aspect, evelation *etc*). These vegetation maps show the reserve's wider surrounding district as predominantly York gum (*Eucalyptus loxophleba*) and wandoo (*E. wandoo*) woodland, while several local upland areas (including A21064) are mapped as wandoo and mallet (*Eucalyptus astringens*) woodland. This is a reasonably accurate representation, although these upland areas also contain significant patches of sheoak (*Allocasuarina huegeliana*). Approximately 20-25 km west of the reserve, wandoo woodland predominates, but marri (*Corymbia calophylla*) and jarrah (*Eucalyptus marginata*) become more common about another 20 km further westwards within Hillman and Godfrey State Forest Blocks (Smith 1974). Powder bark wandoo (*E. accedens*) is more abundant amongst the York gums around the Narrogin area, about 35 km north of the reserve (Beard 1980b). Salmon gum (*E. salmonophloia*) tends to replace wandoo further east (25-35 km), while the Beaufort River area, about 30 km south of the reserve, has a mix of wandoo, yate (*E. occidentalis*), teatree (*Melaleuca* sp.), *Casuarina obesa* and samphire flats (Beard 1980a). Overall, the district was once dominated by open woodlands; however, patches of heath (often *Dryandra* dominated), herbfield and mallee were also relatively common.

Flora surveys of wheatbelt remnants are sparse (Obbens *et al.* 2001). Although not intensive, Muir's (1977a) pioneering surveys of 24 wheatbelt reserves are a notable exception. There are very few flora surveys of remnants from around this district, reflecting the high costs of surveying remnants within this vast wheatbelt region (*i.e.* 18 million hectares). The soon to be released Salinity Action Plan (SAP) surveys will change this situation. While larger remnants (*i.e.* >2000 ha) are certainly important for conserving biodiversity and helping to maintain many of the ecological processes of this region, this paper aims to highlight the important contribution of smaller remnants to regional biodiversity, particularly if they remain intact. A further aim is to present more botanical survey data for this significant region.

Methods

The vegetation communities of Nature Reserve A21064 were interpreted from a 1996 aerial photograph and confirmed in the field during 1999 and 2002. Classification of these vegetation communities is based on Muir (1977b). This classification assesses vegetation structure by taking measures of lifeform/height class and canopy cover/density class to produce a vegetation type. For example, trees 15-30 m with a 10-30% canopy cover were designated woodlands, while the same trees with a canopy cover of 2-10% would be designated as open woodlands. To a significant extent this classification also reflects the species compositional differences. Additionally, brief investigations were made of the soils in each vegetation community. The soil surface was inspected and then shallow holes (3-5 cm depth) were made to assess soil texture and colour.

The flora survey and collections were accomplished by walking along 13 transects (10 spaced at 150 m apart and 3 spaced at 100 m apart) that spanned the full width of the reserve in a north-south orientation. The first transect proceeded in a southerly direction from Noble Road and approximately 50 m in from the reserve's north-east corner. Subsequent transects crossed every vegetation type several times using this technique. This transect survey was undertaken during mid/late spring (*i.e.* October and November 1998). An additional 8 surveys were also carried out between the summer of 1998 and the spring of 2002. On these occasions a 'randomized stratified walk' technique (Hopper *et al.* 1997) was used. This method involves specimen collections via random walks in each vegetation community. The purpose of this intensive surveying was to obtain a voucher specimen of each taxa and to compile a more complete vascular flora list.

All specimens were submitted for incorporation at the WA Herbarium. The species names follow the currently accepted botanical binomials of WACENSUS (WA Herbarium census of Western Australian vascular plants), while conservation status of species is according to the Department of Conservation and Land Management's (CALM) Declared Rare Flora and Priority Flora list (Atkins 2001). The authors also received invaluable information from WA Herbarium database records (WAHERB and FLORABASE). The term "total 'Liliaceae'" refers to the number of closely related, but different new families that have been split from Liliaceae in recent years. For A21064 this includes the families Anthericaceae, Boryaceae and Phormiaceae.

Results

Vegetation and habitat.

Interpretation of the aerial photograph and site survey indicated ten major vegetation communities (Fig 2), including four variants (all explained below). However, there is considerable variability within some communities and at differing locations throughout the reserve. Additionally, there was a range of community boundaries, some very distinct (*e.g.* between pure mallet stands and wandoo woodland or when pure *Allocasuarina huegeliana* stands surround granite-exposed herbfield areas). However, diffuse boundaries have been drawn at roughly midpoint where any two communities overlapped (*e.g.* as demonstrated when Low Woodland and Low Forest communities merge).

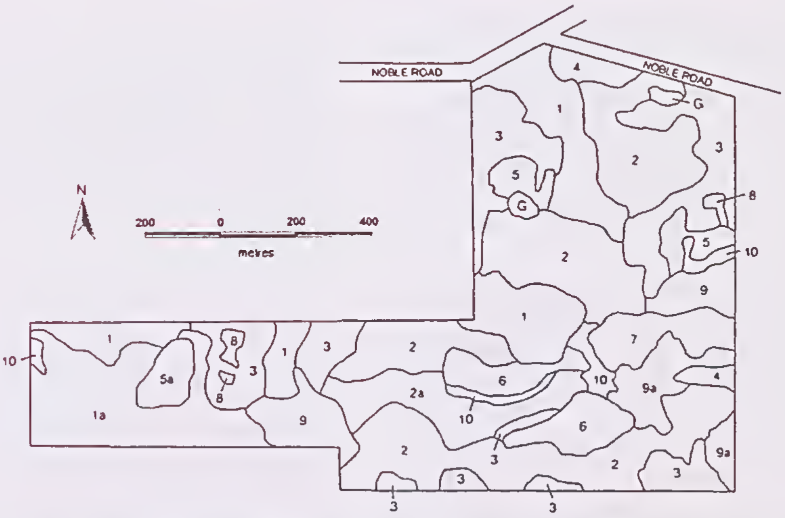

Figure 2. Map of vegetation communities of A21064 Nature Reserve that include 1 and 1a Open Woodland, 2 and 2a Low Woodland, 3 Low Forest, 4 Woodland, 5 and 5a Heath, 6 Low Heath, 7 Thicket (Tall Heath), 8 Herbfield, 9 and 9a Mallet Woodland, 10 Mallee Woodland and G Rehabilitated gravel pits. Communities are described below.

1 Open Woodland. Dominated by *Eucalyptus wandoo* with a generally very open, but variable understorey. This includes areas of almost pure *Gastrolobium trilobum* or *Melaleuca* aff *uncinata* or 'parkland-like' areas with numerous orchids/annuals/grasses and smaller shrubs. Many trees are large to 25 m high with a canopy density about 5 – 15% (*i.e.* very sparse to sparse). Soils are either grey coarse sandy loams or, at the reserve's western end, brown coarse loams with some lateritic gravels. This community represents the top end of shallow drainage lines that form defined creeks further down slope outside the reserve boundaries.

1a Open Woodland. A variant of above, again, dominated by *Eucalyptus wandoo* of generally smaller stature and with a denser canopy cover, about 10 – 25% (*i.e.* sparse). Lying entirely on lateritic ridge country, it demarcates itself from community 1 along the line of a small breakaway. A sparse to mid dense understorey of predominately *Dryandra* species occur on exposed lateritic boulders with residual soils on the top edge of the breakaway and up slope at the ridgeline. Elsewhere is fairly open with various scattered shrubs and some annuals on soils of red-brown clay loam with numerous gravels.

2 Low Woodland. A mixed woodland with a mid dense canopy cover (*i.e.* about 30 – 70%) consisting of almost equal proportions of *Eucalyptus wandoo* (up to 20 m high) and *Allocasuarina huegeliana* on grey-brown sandy loams sometimes with varying amounts of gravel. Understorey is variable including open areas of low shrubs, annuals and some grasses to mid dense areas of *Acacia* or *Gastrolobium*.

2a Low Woodland. A mixed woodland variant of above with mid dense canopy consisting of *Eucalyptus wandoo* (up to 20 m high) and interspersed individuals or patches of *Eucalyptus astringens* subsp *astringens* (Brown Mallet) and occasionally with scattered *Allocasuarina huegeliana*. Again, a variable understorey ranging mostly open to mid dense in parts. Soils are red-brown coarse clay loams with gravels and sometimes there is exposed lateritic hardcap.

3 Low Forest. Predominantly pure stands of *Allocasuarina huegeliana* with occasional scattered *Eucalyptus wandoo* and generally mid dense to dense canopy cover (*i.e.* > 70%). Soils are grey-brown to red-brown sandy or clayey sand loams sometimes with a little gravel. The understorey canopy cover is open to mid dense, including numerous annuals and commonly a tall *Lepidosperma* sp (FO204/98), *Agrostocrinum scabrum* and *Hypocalymma angustifolium*. This community occurs where granite is close to the surface and often outcropping or boulder stacks are nearby.

4 Woodland. Composed of pure stands of tall (*i.e.* 25 – 30 m) *Eucalyptus longicornis* with a very sparse understorey of *Acacia erinacea*, *Acacia lasiocarpa* var. *sedifolia*, a few sedges and annuals found on red-brown clay loams. These areas appear to be associated with shallow drainage zones.

5 Heath. A heath of mid dense to dense canopy cover containing a diverse mix of shrubs about 1 – 2 m high on grey-brown sandy clay loams with some gravel content. The families Myrtaceae, Proteaceae, Goodeniaceae, Papilionaceae and Stylidiaceae are well represented along with many others. This community occurs on the gentle mid slope areas of the reserve and never appears on the ridge top.

5a Heath. A variant of the above comprising a diverse mix of shrubs (about 1 – 2 m) with interspersed emergent shrubs (to about 3.5 m) namely *Dryandra sessilis* and *Nuytsia floribunda*. This unusual combination occurs on a localised sheet of white sand, which probably overlays lateritic and/or granitic profiles seen adjacent to this community. *Eremaea pauciflora* dominates although many other species are present.

6 Low Heath. A very diverse mix of small to mid sized shrubs (about 0.25 – 1.5 m) with a mid dense canopy cover found on white-grey clayey loams with occasional gravel content. This soil profile is possibly exposed and eroding kaolin, and occurs extensively on lower parts of the flattened ridgeline. This community contains the same families as outlined for community 5; however, it also has a marginally greater diversity of taxa than the above heaths.

7 Thicket (Tall Heath). Comprising a dense mix of taller shrubs (about 1.5 – 3.0 m) dominated by Dryandra, particularly *D. armata* and *D. nobilis*, but including some other tall Proteaceae species (*e.g. Adenanthos cygnorum* and *Hakea trifurcata*) and occasionally interspersed mallees. These thickets are located on the flattened ridgeline. The soils are red-brown to grey-brown coarse clayey loams or sandy loams with abundant lateritic gravels, rocks and some exposed hardcap.

8 Herbfield. Exposed or near-surface granite sheets with some residual surface soil or soil pockets frequently covered by *Borya sphaerocephala*, mosses and lichens, but including numerous annual herbs and some sedges. Generally abutting or surrounded by *Allocasuarina* woodland.

9 Mallet Woodland. Dense pure stands of *Eucalyptus astringens* subsp *astringens* (about 10 to 20 m) with an almost absent understorey except for a few resilient shrubs and abundant bark litter. Soils are red-brown to brown coarse clay loams with numerous gravels. All occurrences in the reserve are on the ridgeline including one area adjacent to and on a lateritic breakaway slope.

9a Mallet Woodland. This community, a variant of the above, comprises more open and generally taller (about 15 to 25 m) stands of *Eucalyptus astringens* subsp *astringens* often interspersed with *E. wandoo* or *Allocasuarina huegeliana* and with variable canopy cover ranging from open to mid dense. The open to mid dense understorey includes *Acacia celastrifolia, A. pulchella, Nemcia obovata, Dryandra nobilis* and many others. Soils are red-brown to grey-brown clayey loams containing numerous gravels with rocks/hardcap regularly occurring within this ridgeline community.

10 Mallee Woodland. Consisting of various mallee species, but occasionally pure stands to 4 m high and sometimes with other tree species interspersed or with tall shrubs. In the western end of the reserve these mallees tend to be *Eucalyptus aspersa, E. falcata, E. latens* and *E. thamnoides* subsp *megista* while in other areas mainly *E. incrassata* and *E. pluricaulis* subsp *pluricaulis*. This community is located either on the ridge or the adjacent upper slope areas where the soils are red-brown loams with gravels. .

G Rehabilitated gravel pits. Old gravel extraction sites that have been deep ripped and allowed to regenerate naturally. At this stage, the flora comprises mainly pioneer species and limited occurrences of several weed species.

Flora.

A total of 323 vascular plant taxa (including 22 weed species) from 51 families was listed for Nature Reserve A21064 with dicots and shrub species being the predominant taxa for the reserve (Table 1).

The most represented families were Myrtaceae (39), Proteaceae (29), Papilionaceae (26), Orchidaceae (26), Poaceae (20), total 'Liliaceae' (20), Asteraceae (17), Stylidaceae (17), Cyperaceae (16), and Goodeniaceae (12). Nine Poaceae and three Asteraceae species recorded are weeds.

The genera with the greatest number of species were *Stylidium* (15), *Eucalyptus* (12), *Acacia* (10), *Caladenia* (9), *Hakea* (8), *Lepidosperma* (8), *Dryandra* (7), *Drosera* (6) and *Austrostipa, Leucopogon, Dampiera, Goodenia, Melaleuca, Daviesia* and *Petrophile* with five species each.

One declared rare species (*Conostylis drummondii*) and seven priority species (*Dryandra rufistylis, Eucalyptus aspersa, E. latens, Leucopogon florulentus, L* sp Dongolocking, *Microcorys lenticularis* and *Thysanotus cymosus*) were recorded for the reserve.

Discussion

Vegetation and habitat.

The vegetation of the reserve is not unique because similar vegetation types or variants thereof can be found in other upland remnants in this region. Overall the vegetation of the reserve is relatively pristine and contains a wide representation of upland communities for its small size. This alone makes it quite special in

Table 1

Plant type and lifeform for all taxa collected at A21064.

Taxa	Total	Dicotyledons	Monocotyledons	Gymnosperms	Pteridophytes
Families	51	37	12	1	1
Genera	155	98	55	1	1
Taxa:					
(a) native	301	211	88	1	1
(b) exotic	22	11	11	0	0
Lifeform					
Tree	8	8	0	0	0
Mallee/Tree	1	1	0	0	0
Mallee	7	7	0	0	0
Tall shrub	19	18	0	1	0
Low shrub	113	112	1	0	0
Herb (annual)	42	33	9	0	0
Herb (perennial)	127	37	89	0	1
Vine	6	6	0	0	0
TOTAL	323				

terms of value as public conservation estate. These woodlands can be moderately diverse due to the abundant annuals present, but more frequently it is the open heaths and patches of other communities within these woodlands that account for the greater proportion of species diversity, particularly perennial species (Yates *et al.* 1999). Table 1 also reaffirms this with 131 perennial shrub taxa listed, the next highest being perennial herbs at 127 taxa, but with significantly less vegetative cover overall than the shrubs produce.

Flora.

We consider Nature Reserve A21064, with 323 taxa located within 110 ha, as exceptionally diverse for an upland area. It is always difficult to compare flora surveys because of the different methodologies applied, the differences in the vegetation communities surveyed and the differences in surveying intensity and season (Obbens *et al.* 2001). Nonetheless, a quadrat-based flora survey of 3 remnants within the Cartmeticup sub-catchment, Shire of Woodnilling (about 35 km south-east of A21064) by Gunness (1999) found 266 vascular taxa in 130 ha although less than 40% of this survey was upland habitat. In 2001, the Western Australian Herbarium had 358 individual vascular plant species recorded for the Highbury State Forest, a large collection of woodland remnants (4028 ha) with significant upland areas just south of Narrogin (about 20 km north of A21064). For this survey, we found new taxa on every visitation and even after many visits the last survey still produced over 30 new taxa. Our experience is that intense surveying appears to overcome the shortfalls of annual/seasonal variation or of detecting cryptic/short-lived species *etc.* Most surveys do not have the resources for such intensive work and hence record significantly less. In fact, Nilsson & Nilsson (1985) reported that standardised surveys by professional botanists estimate only 79% at best of total plant diversity. Consequently, most survey results somewhat underrate the biodiversity present and hence the conservation value of the areas surveyed. Even this intensive surveying program cannot be considered as 100% conclusive in detecting all the vascular plant taxa within A21064.

Declared Rare Flora.

One declared rare taxon (*Conostylis drummondii*) is listed for the reserve. Within the reserve it occurs in one heath community only, while there are several populations recorded mostly on roadside situations (WAHERB data). This species has an IUCN ranking of endangered.

Priority species.

Seven priority taxa have been identified and, along with the rare flora, reaffirming the high conservation value of the reserve.

Dryandra rufistylis. Priority 2. Seven small or medium sized populations are known from degraded roadsides mainly around Woodanilling with a few populations recorded further east to Nyabing. The A21064 population is the most western population and the second to be discovered on a reserve.

Eucalyptus aspersa. Priority 4. A reasonably widespread mallee species (77 WAHERB collections) ranging from Julimar State Forest in the north to Frankland in the south. Most populations are apparently small groves and distributed unevenly.

Eucalyptus latens. Priority 4. Again, this is a fairly widespread mallee species (57 WAHERB collections). The four limits of its distribution are roughly North Bannister, Kulin, Tarin Rock and Arthur River/Darkin area. Most populations have small numbers of individuals.

Leucopogon florulentus. Priority 2. This taxon is currently under review (M Hislop, WA Herbarium). There is some taxonomic uncertainty regarding the boundaries of this species, with two variants noted. The more western/inland variant (*i.e.* Bannister, Cordering, Dryandra State Forest, Dumbleyung and A21064) is potentially a different taxon from the more eastern/south coastal variant (*i.e.* Ongerup to east of Esperance) which represents the typical *L. florulentus* populations. At present, the A21064 population consisting of thousands of plants represents a significant find.

Leucopogon sp Dongolocking. Priority 2. This taxon belongs to the 'Gynoconus' group of Leucopogons and is most closely related to *L. pogonocalyx* and another unnamed taxon *L.* sp Wandering (M Hislop, WA Herbarium personal communication). It is currently known from two localities, Dongolocking and A21064 nature reserves. The species has a low sprawling habit and is difficult to find amongst other shrubs, so numbers of individuals in the A21064 populations are not exactly known at present.

Microcorys lenticularis. Priority 2. There are several populations of this taxon in scattered locations ranging from Hyden in the east to Boxwood Hills in the south to Tarin Rock and Ongerup areas. A21064 is now an additional population and the most western distribution for the species. Most populations have few individuals and are located on degraded roadsides.

Thysanotus cymosus. Priority 3. First collected by NH Brittan in 1958 south of Kulin. There are now five known locations (*i.e.* Popanyinning, Muntadgin, Hyden, north of Kojonup and A21064). *Thysanotus cymosus* appears to grow in sandy clay loams often associated with nearby granite outcrops.

Species of interest.

A small shrub with yellow/dark brown pea flowers was listed as *Pultenaea* aff *ericifolia*. This unnamed species belongs to the *Pultenaea verruculosa/ericifolia* group of species currently under taxonomic revision. It is probably closely related to the south coast species that has been known erroneously as *P. vestita*. The true *P. vestita* does not occur in Western Australia (M Hislop, WA Herbarium personal communication). However, this specimen and another northern collection differ from *P. vestita* in having distinctive recurved leaf tips and different floral bract morphology.

Two variants of *Baeckea crispiflora* occur within the reserve, one with the usual narrow leaf and the other a wider, round-leafed variant (probably another unnamed taxon; M Trudgen, WA Herbarium personal communication). Rounded and pointed leaf variants of *Synaphea* aff *interioris* have also been recorded. Range extensions were recorded for *Allocasuarina campestris*, *Desmocladus fascicularis, Dryandra lindleyana* subsp *sylvestris, Stylidium carnosum, Tetraria octrandra* and *Thelymitra crinita*. Most range extensions were significant increases in easterly occurrence for species with a deep southwest distribution, while only *Allocasuarina campestris* significantly increased its westerly position from its more inland distribution.

Patterns of species distributions

The A21064 locality represents the limits of distribution for a number of taxa including *Eucalyptus argyphea* (western edge), *Lomandra suaveolens* and *Hemiandra linearis* (eastern edge), and *Conospermum stoechadis* subsp. *sclerophyllum* and *Isopogon dubius* (southern edge). Approximately 24% of the reserve's species list have a distribution pattern located within the wetter portion of the South West Botanical Province (*i.e.* roughly NW/SW orientated, often occurring near coastal and extending inland to the inner/mid wheatbelt regions). Another 28% have a similar orientated distribution pattern, but these are located within the drier portion of the South West Botanical Province (*i.e.* occurring from the inner/mid wheatbelt areas and extending eastwards and sometimes overlapping into the more arid Eremaean Province). The latter distribution pattern frequently extends to the coast north of the Eneabba area or to the coast east of Albany. A widespread distribution within the South West Botanical Province and adjacent Eremaean Province accounted for 22% of the species distributions of the reserve. Additional distribution patterns include the geographically restricted (*i.e.* about 100-150 km radius) accounting for 6% of the reserve's flora, south coastal and adjacent agricultural districts accounting for 5%, localised distributions (*i.e.* about 50 km radius) accounting for 3% while various other distributions accounted for the remainder.

The first two patterns of distribution accounted for 52% of the taxa listed for the reserve and are common distribution patterns for many taxa of the southwest. The area where the edges of these distributions overlap represents a 'transitional zone'. A21064 sits squarely within this narrow zone. It is also located within the western limits of Beard's 1980 map of the South West Botanical Province's Avon district.

Introduced weeds.

There were 22 weed species (about 6.8% of the flora) recorded for the reserve, most occurring in disturbed boundary areas adjacent to farmland or beside tracks or within old gravel extraction pits. Many are common agricultural weeds such as the broadleafs *Arctotheca calendula* (Capeweed), *Hypochaeris glabra* (Flatweed), *Erodium botrys* and *Trifolium campestre*, or grasses, such as *Avena barbata, Bromus diandrus* and *Lolium rigidium*. Although weeds are common in these boundary areas their extent elsewhere is very limited, apart from the orchid *Disa bracteata* which is scattered throughout several communities. Overall, the vast majority of the reserve is in near pristine condition.

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Appendix 1

The vascular plant taxa recorded for A21064 Nature Reserve listed in alphabetical order by family. Threatened or priority status of taxa is recorded for those relevant species. The * symbol represents species which are naturalized weeds. The collector's number for each specimen is included in parentheses after species authority name.

Adiantaceae
Cheilanthes austrotenuifolia HM Quirk & TC Chambers (FO218/98)

Amaranthaceae
Ptilotus declinatus Nees (FO72/02)
Ptilotus manglesii (Lindl) F Muell (LWS1099)

Anthericaceae
Agrostocrinum scabrum (R Br) Baill (FO228/98)
Caesia occidentalis R Br (LWS1411)
Chamaescilla corymbosa (R Br) Benth. (FO310/99)
Chamaescilla spiralis (Endl) Benth (LWS1236)
Corynotheca micrantha var *elongata* RJF Hend (LWS1414)
Dichopogon fimbriatus (R Br) JF Macbr (LWS1410)
Laxmannia grandiflora Lindl (FO40/01)
Laxmannia squarrosa Lindl (LWS1217)
Sowerbaea laxiflora Lindl (FO321/99)
Thysanotus cymosus Brittan (P3) (FO50/02)
Thysanotus patersonii R Br (FO331/99)
Thysanotus thyrsoideus Baker (FO281/98)
Tricoryne elatior R Br (FO279/98)

Apiaceae
Trachymene ornata (Endl) Druce (FO319/99)
Trachymene pilosa Sm (FO215/98)

Asteraceae
* *Arctotheca calendula* (L) Levyns (FO222/98)
Argentipallium niveum (Steetz) Paul G Wilson (LWS1098)
Blennospora drummondii A Gray (FO324/99)
Brachyscome glandulosa (Steetz) Benth (FO34/01)
Helichrysum leucopsideum DC (FO274/98)
* *Hypochaeris glabra* L (FO233/98)
Lagenophora huegelii Benth (LWS1499)
Lawrencella rosea Lindl (FO333/99)
Millotia tenuifolia Cass var *tenuifolia* (FO38/01)
Podolepis canescens DC (LWS1096)
Podolepis gracilis (Lehm) Graham (LWS1095)
Podolepis lessonii (Cass) Benth (FO304/99)
Pterochaeta paniculata Steetz (FO302/98)
Rhodanthe citrina (Benth) Paul G Wilson (LWS1097)
Rhodanthe manglesii Lindl (LWS1093)
Siloxerus multiflorus (Nees) PS Short (FO28/01)
* *Ursinia anthemoides* (L) Poir (FO230/98)

Boryaceae
Borya sphaerocephala R Br (FO234/98)

Casuarinaceae
Allocasuarina campestris (Diels) LAS Johnson (FO67/02)
Allocasuarina huegeliana (Miq) LAS Johnson (LWS1247)
Allocasuarina humilis (Otto & F Dietr) LAS Johnson (LWS1246)
Allocasuarina microstachya (Miq) LAS Johnson (FO250/98)

Crassulaceae
Crassula colorata (Nees) Ostenf (FO225/98B)
Crassula decumbens Thunb (FO35/01)
Crassula exserta (Reader) Ostenf (FO225/98A)

Cupressaceae
Callitris roei (Endl) F Muell (FO2/01)

Cyperaceae
Caustis dioica R Br (FO21/01)
Lepidosperma aff *costale* (LWS1431)
Lepidosperma brunonianum Nees (FO287/98)
Lepidosperma costale Nees (FO205/98)
Lepidosperma leptostachyum Benth (FO252/98)
Lepidosperma sp (small sedge) (FO203/98)
Lepidosperma sp (large sedge around granites) (FO204/98)
Lepidosperma sp K Boorabbin (KL Wilson 2579) (LWS1432)
Lepidosperma tuberculatum Nees (LWS1503)
Mesomelaena stygia (R Br) Nees subsp *stygia* (FO32/01)
Schoenus aff *brevisetis* (FO260/98)
Schoenus aff *subflavus* (FO48/02)
Schoenus armeria Boeck (FO251/98)
Schoenus minutulus F Muell (LWS1422)
Tetraria capillaris (F Muell) JM Black (FO259/98)
Tetraria octandra (Nees) Kuk (LWS1224)

Dasypogonaceae
Chamaexeros serra (Endl) Benth (FO293/98)
Lomandra effusa (Lindl) Ewart (FO24/01)
Lomandra micrantha (Endl) Ewart subsp *micrantha* (LWS1427)
Lomandra suaveolens (Endl) Ewart (LWS1519)

Dilleniaceae
Hibbertia aff *recurvifolia* (FO262/98)
Hibbertia commutata Steud (LWS1238)
Hibbertia hemignosta (Steud) JR Wheeler (LWS1417)
Hibbertia microphylla Steud (FO309/99)
Hibbertia rupicola (S Moore) CA Gardner (LWS1062)

Droseraceae
Drosera androsacea Diels (FO326/99)
Drosera bulbosa Hook subsp *bulbosa* (FO28/99)
Drosera glanduligera Lehm (FO12/01)
Drosera macrantha Endl subsp *macrantha* (FO13/01)
Drosera menziesii DC subsp *menziesii* (FO332/99)
Drosera subhirtella Planch (FO322/99)

Epacridaceae
Andersonia parvifolia R Br (FO62/02)
Astroloma cataphractum AJG Wilson ms (FO20/99)
Astroloma serratifolium (DC) Druce (FO229/98)
Leucopogon cymbiformis DC (LWS1440)
Leucopogon dielsianus E Pritz (LWS1516)
Leucopogon fimbriatus Stschegl (FO8/01)
Leucopogon florulentus Benth (P2) (FO22/99)
Leucopogon sp Dongolocking (P2) (LWS1495)
Lysinema ciliatum R Br (FO323/99)

Fumariaceae
* *Fumaria capreolata* L (FO29/01)

Geraniaceae
* *Erodium botrys* (Cav) Bertol (FO83/02)
Pelargonium havlasae Domin (FO209/98)

Goodeniaceae
Anthotium odontophyllum Sage (LWS1409)
Dampiera haematotricha de Vriese subsp *haematotricha* (LWS1058)
Dampiera juncea Benth (LWS1057)
Dampiera lavandulacea Lindl (LWS1056)
Dampiera lindleyi de Vriese (LWS1055)
Dampiera sacculata Benth (FO55/02)
Goodenia incana R Br (LWS1054)
Goodenia pulchella subsp Wheatbelt (LW Sage & F Hort 795) (LWS1059)
Goodenia scapigera R Br subsp *scapigera* (LWS1060)
Goodenia watsonii subsp *glandulosa* Carolin (LWS1406)
Lechenaultia biloba Lindl (FO277/98)
Velleia trinervis Labill (LWS1061)

Haemodoraceae
Anigozanthos humilis Lindl subsp *humilis* (LWS1066)
Conostylis aculeata subsp *bromelioides* (Endl) JW Green (LWS1087)
Conostylis drummondii Benth (R) (FO61/02)
Conostylis pusilla Endl (LWS1086)
Haemodorum discolor T Macfarlane (LWS1434)

Haloragaceae
Glischrocaryon aureum (Lindl) Orchard (FO11/02)

Hypoxidaceae
Hypoxis glabella R Br var *glabella* (FO1/01)

Iridaceae
Orthrosanthus laxus var *gramineus* (Endl) Geerinck (FO306/99)
Patersonia juncea Lindl (FO283/98)
Patersonia occidentalis R Br (LWS1089)
* *Romulea rosea* (L) Eckl (FO220/98)

Lamiaceae
Chloanthes coccinea Bartl (LWS1065)
Hemiandra linearis Benth (FO57/02)
Hemigenia humilis Benth (FO68/02)
Hemigenia incana (Lindl) Benth (LWS1072)
Microcorys lenticularis F Muell (P2) (FO85/02)

Lobeliaceae
Isotoma hypocrateriformis (R Br) Druce (FO210/98)
Lobelia rarifolia E Wimm (FO47/02)

Loganiaceae
Phyllangium sulcatum Dunlop (FO320/99)

Loranthaceae
Nuytsia floribunda (Labill) Fenzl (LWS1517)

Mimosaceae
Acacia acuminata Benth (FO257/98)
Acacia applanata Maslin (FO37/01)
Acacia browniana var *intermedia* (E Pritz) Maslin (FO289/98)
Acacia celastrifolia Benth (LWS1426)
Acacia erinacea Benth (LWS1237)
Acacia lasiocalyx CRP Andrews (FO11/01)
Acacia lasiocarpa var *sedifolia* (Meisn) Maslin (LWS1248)
Acacia microbotrya Benth (FO16/99)
Acacia pulchella var *glaberrima* Meisn (FO286/98)
Acacia stenoptera Benth (FO25/99)

Myrtaceae
Baeckea crispiflora F Muell (round leaf variant) (FO78/02)
Baeckea crispiflora F Muell (narrow leaf variant) (FO76/02)
Baeckea preissiana (Schauer) Domin (FO272/98)
Beaufortia bracteosa Diels (LWS1212)
Beaufortia incana (Benth) AS George (LWS1206)
Beaufortia micrantha var *puberula* Benth (LWS1424)
Callistemon phoeniceus Lindl (LWS1419)
Calothamnus planifolius Lehm (LWS1220)
Calothamnus quadrifidus R Br (LWS1219)
Calothamnus sanguineus Labill (FO3/01)
Calytrix breviseta subsp *stipulosa* (W Fitzg) Craven (LWS1202)
Calytrix leschenaultii (Schauer) Benth (FO318/99)
Eremaea pauciflora (Endl) Druce var *pauciflora* (LWS1423)
Eucalyptus argyphea LAS Johnson & KD Hill (FO69/02)
Eucalyptus aspersa Brooker & Hopper (P4) (LWS1442)
Eucalyptus astringens (Maiden) Maiden subsp *astringens* (FO27/01)
Eucalyptus falcata Turcz subsp *falcata* (LWS1243)
Eucalyptus incrassata Labill (LWS1208)
Eucalyptus latens Brooker (P4) (LWS1441)
Eucalyptus longicornis (F Muell) Maiden (LWS1491)
Eucalyptus phenax Brooker & Slee (FO73/02)
Eucalyptus pluricaulis Brooker & Hopper subsp *pluricaulis* (LWS1508)
Eucalyptus thamnoides subsp *megista* Brooker & Hopper (LWS1507a)
Eucalyptus uncinata Turcz (FO71/02)
Eucalyptus wandoo Blakely subsp *wandoo* (LWS1510)
Hypocalymma angustifolium (Endl) Schauer (LWS1200)
Kunzea micromera Schauer (FO305/99)
Kunzea preissiana Schauer (LWS1201)
Leptospermum erubescens Schauer (FO244/98)
Melaleuca aff *uncinata* (FO266/98)
Melaleuca lecanantha Barlow (FO212/98)
Melaleuca subtrigona Schauer (LWS1211)
Melaleuca tuberculata Schauer var *tuberculata* (LWS1210)
Melaleuca viminea Lindl subsp *viminea* (FO13/02)
Rinzia fumana Schauer (LWS1226)
Verticordia densiflora Lindl var *densiflora* (LWS1436)
Verticordia grandiflora Endl (LWS1092)
Verticordia huegelii var *stylosa* (Turcz) AS George (FO75/02)
Verticordia insignis subsp *compta* (Endl) AS George (LWS1213)

Olacaceae
Olax benthamiana Miq (FO19/01)

Orchidaceae
Caladenia aff *marginata* (FO26/99)
Caladenia exilis Hopper & AP Br subsp *exilis* (FO45/01)
Caladenia falcata (Nicholls) MA Clem & Hopper (LWS1084)
Caladenia flava R Br subsp *flava* (FO328/99)
Caladenia flava x *reptans* (FO31/01)
Caladenia longicauda subsp *eminens* (Domin) Hopper & AP Br (FO338/99)
Caladenia reptans Lindl subsp *reptans* (FO16/01)
Caladenia saccharata Rchb f (FO36/01)
Caladenia xantha Hopper & AP Br (FO14/01)
Cyanicula deformis (R Br) Hopper & AP Br (FO17/01)
Cyanicula sericea (Lindl) Hopper & AP Br (FO33/01)
* *Disa bracteata* Sw (LWS1413)
Diuris corymbosa Lindl (FO337/99)
Diuris setacea R Br (FO278/98)
Elythranthera brunonis (Endl) AS George (LWS1239)
Eriochilus dilatatus subsp *multiflorus* (Lindl) Hopper & AP Br ms (FO27/99)
Eriochilus sp (LWS1520)
Leporella fimbriata (Lindl) AS George (LWS1506)
Oligochaetochilus sanguineus (DL Jones & MA Clem) Szlach (LWS1492)
Oligochaetochilus vittatus (Lindl) Szlach (FO335/99)
Prasophyllum gracile Lindl (FO336/99)
Prasophyllum parvifolium Lindl (LWS1505)
Pterostylis aff *nana* (LWS1500)
Pterostylis recurva Benth (FO9/01)
Thelymitra antennifera (Lindl) Hook f (FO15/01)
Thelymitra crinita Lindl (FO82/02)

Oxalidaceae
* *Oxalis corniculata* L (FO211/98)

Papilionaceae
Bossiaea eriocarpa Benth (FO208/98)

Chorizema aciculare (DC) CA Gardner subsp *aciculare* (FO327/99)
Daviesia articulata Crisp (FO91/02)
Daviesia cardiophylla F Muell (FO22/01)
Daviesia decipiens (E Pritz) Crisp (LWS1502)
Daviesia hakeoides subsp *subnuda* (Benth) Crisp (FO246/98)
Daviesia longifolia Benth (FO84/02)
Dillwynia sp A Perth Flora (R Coveny 8036) (FO25/01)
Gastrolobium calycinum Benth (LWS1069)
Gastrolobium parviflorum (Benth) Crisp (FO240/98)
Gastrolobium stowardii S Moore (FO271/98)
Gastrolobium trilobum Benth (FO269/98)
Gompholobium marginatum R Br (FO248/98)
Gompholobium tomentosum Labill (FO56/02)
Hovea pungens Benth (FO18/01)
Isotropis cuneifolia (Sm) Heynh (FO330/99)
Isotropis drummondii Meisn (LWS1063)
Jacksonia alata Benth (LWS1067)
Jacksonia racemosa Meisn (LWS1421)
Jacksonia sternbergiana Huegel (LWS1241)
Mirbelia dilatata R Br (LWS1068)
Nemcia aspera Crisp ms (LWS1415)
Nemcia obovata (Benth) Crisp (LWS1070)
Pultenaea aff *ericifolia* (FO26/01)
* *Trifolium arvense* L var *arvense* (FO77/02)
* *Trifolium campestre* Schreb var *campestre* (FO60/02)

Phormiaceae
Dianella revoluta var *divaricata* (R Br) RJF Hend (LWS1498)
Stypandra glauca R Br (LWS1214)

Pittosporaceae
Billardiera sericea (Turcz) EM Benn (FO54/02)
Marianthus bicolor (Putt) F Muell (FO24/99)
Marianthus erubescens Putt (LWS1418)
Sollya fusiformis (Labill) Payer (FO256/98)

Poaceae
* *Aira cupaniana* Guss (FO226/98)
Amphipogon strictus R Br (FO231/98)
Amphipogon turbinatus R Br (FO232/98)
Austrodanthonia caespitosa (Gaudich) HP Linder (LWS1231)
Austrodanthonia setacea (R Br) HP Linder (LWS1425)
Austrostipa elegantissima (Labill) SWL Jacobs & J Everett (FO242/98)
Austrostipa hemipogon (Benth) SWL Jacobs & J Everett (LWS1230)
Austrostipa mollis (R Br) SWL Jacobs & J Everett (FO52/02)
Austrostipa tenuifolia (Steud) SWL Jacobs & J Everett (FO81/02)
Austrostipa variabilis (Hughes) SWL Jacobs & J Everett (LWS1232)
* *Avena barbata* Link (FO238/98)
* *Briza maxima* L (FO223/98)
* *Briza minor* L (LWS1429)
* *Bromus diandrus* Roth (FO236/98)
* *Bromus rubens* L (FO80/02)
* *Ehrharta longiflora* Sm (FO235/98)
* *Lolium rigidum* Gaudin (FO239/98)
Neurachne alopecuroidea R Br (LWS1233)
Poa drummondiana Nees (LWS1433)
* *Vulpia myuros* (L) CC Gmel (FO51/02)

Polygalaceae
Comesperma ciliatum Steetz (FO70/02)
Comesperma integerrimum Endl (LWS1235)
Comesperma scoparium Steetz (FO20/01)

Portulacaceae
Calandrinia calyptrata Hook f (FO74/02)

Primulaceae
* *Anagallis arvensis* L (FO217/98)

Proteaceae
Adenanthos cygnorum Diels subsp *cygnorum* (FO4/01)
Banksia sphaerocarpa R Br var *sphaerocarpa* (LWS1249)
Conospermum stoechadis subsp *sclerophyllum* (Lindl) EM Benn (LWS1218)
Dryandra armata R Br var *armata* (LWS1221)
Dryandra fraseri R Br var *fraseri* (LWS1222)
Dryandra lindleyana subsp *sylvestris* AS George (LWS1437a)
Dryandra nivea (Labill) R Br subsp *nivea* (LWS1244b)
Dryandra nobilis Lindl subsp *nobilis* (FO18/99)
Dryandra rufistylis AS George (P2) (LWS1437b)
Dryandra sessilis (Knight) Domin (FO268/98)
Hakea brownii Meisn (FO17/99)
Hakea hastata Haegi (LWS1496)
Hakea incrassata R Br (FO201/98)
Hakea lehmanniana Meisn (FO255/98)
Hakea lissocarpha R Br (FO21/99)
Hakea prostrata R Br (LWS1513)
Hakea trifurcata (Sm) R Br (FO284/98)
Hakea undulata R Br (LWS1514)
Isopogon dubius (R Br) Druce (LWS1205)
Isopogon teretifolius R Br subsp *teretifolius* (LWS1244a)
Persoonia quinquenervis Hook (LWS1234)
Petrophile rigida R Br (FO43/01)
Petrophile seminuda Lindl (FO294/98)
Petrophile serruriae R Br (LWS1204)
Petrophile squamata R Br subsp *squamata* (FO307/99)
Petrophile striata R Br (FO42/01)
Stirlingia simplex Lindl (LWS1074)
Synaphea aff *interioris* (pointed leaf variant) (FO41/01)
Synaphea aff *interioris* (rounded leaf variant) (FO30/01)

Restionaceae
Desmocladus asper (Nees) BG Briggs & LAS Johnson (FO292/98)
Desmocladus fasciculatus (R Br) BG Briggs & LAS Johnson (FO58/02)
Harperia lateriflora W Fitzg (FO87/02)
Hypolaena exsulca R Br (LWS1227)
Lepidobolus preissianus Nees subsp *preissianus* (LWS1223)
Lyginia imberbis R Br (LWS1229)

Rhamnaceae
Cryptandra arbutiflora Fenzl (FO308/99)
Cryptandra myriantha Diels (LWS1494)
Cryptandra pungens Steud (FO39/01)
Trymalium ledifolium var *rosmarinifolium* (Steud) Benth (LWS1497)

Rubiaceae
Opercularia vaginata Juss (FO227/98)

Rutaceae
Boronia crassifolia Bartl (FO65/02)

Santalaceae
Choretrum glomeratum var *chrysanthum* (F Muell) Benth (FO12/02)
Santalum acuminatum (R Br) A DC (LWS1512)

Sapindaceae
Dodonaea humifusa Miq (FO44/01)
Dodonaea pinifolia Miq (FO247/98)

Scrophulariaceae
* *Parentucellia latifolia* (L) Caruel (FO219/98)

Stackhousiaceae
Stackhousia monogyna Labill (FO214/98)
Stackhousia scoparia Benth (FO64/02)

Sterculiaceae
Thomasia macrocalyx Steud (FO270/98)

Stylidiaceae
Levenhookia pusilla R Br (LWS1451)

Levenhookia stipitata (Sond) F Muell (FO224/98)
Stylidium calcaratum R Br (FO334/99)
Stylidium caricifolium Lindl (LWS1081)
Stylidium carnosum Benth (LWS1075)
Stylidium dichotomum DC (FO207/98)
Stylidium eriopodum DC (FO59/02)
Stylidium hirsutum R Br (LWS1082)
Stylidium leptophyllum DC (LWS1079)
Stylidium luteum subsp *clavatum* Carlquist (LWS1077)
Stylidium petiolare Sond (FO325/99)
Stylidium piliferum R Br (LWS1080)
Stylidium pubigerum Sond (LWS1076)
Stylidium repens R Br (FO282/98)
Stylidium rhynchocarpum Sond (FO89/02)
Stylidium squamellosum DC (FO49/02)
Stylidium uniflorum Sond (LWS1078)

Thymelaeaceae
Pimelea suaveolens Meisn subsp *suaveolens* (LWS1091)
Pimelea sulphurea Meisn (FO66/02)

Tremandraceae
Tetratheca virgata Steetz (LWS1064)

Xanthorrhoeaceae
Xanthorrhoea gracilis Endl (FO264/98)

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Five years monitoring of the Lake Muir-Unicup wetland system, south-western Australia

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Abstract

The vegetation of 27 wetlands was monitored over a five year period (1997 to 2002) in the Lake Muir-Unicup system east of Manjimup, where salinization has been reported over the last decade. Initial results suggest that only three wetlands have deteriorated over this period. However given the lag times known to occur in groundwater movements and the appearance of new saline seeps in the catchment, it is unlikely that the ground water system is yet in equilibrium. There is an urgent need for ground water management programs to be developed to protect biodiversity values. Detailed hydrological mapping of the catchment is currently underway.

Keywords: Monitoring, wetlands, salinity, Muir-Unicup catchment

Introduction

Dryland salinity is one of the most serious concerns for conservation management in the South West Botanical Province (George *et al.* 1995) which has been recognized as one of the world's 25 biodiversity hotspots under threat (Myres *et al.* 2000). The salinity problem has arisen as a result of the large scale clearance of perennial native vegetation for annual cereal crop and pasture production with the subsequent rise in water tables and mobilization of salt that was previously confined deep in the soil profiles. Because of their position low in the landscape, wetlands are generally considered one of the first habitats to be impacted by rising saline ground water. The problems in wetlands are often exacerbated by drainage works.

In 1996 the Western Australian Government released a Salinity Action Plan to address a number of issues arising from salinity (Government of Western Australia 1996). One of the strategies was to designate recovery catchments which would be allocated resources to protect biodiversity values. The Lake Muir-Unicup system of wetlands was one of the first identified, on the basis of outstanding fauna and flora values (Australian Nature Conservation Agency 1996; Gibson & Keighery 2000). Based on these same data the Muir-Byenup system, south of the Muir Highway, was subsequently nominated (Government of Western Australia 2000) and listed (Wetlands International 2002) as a Ramsar wetland of international importance.

In 1997 a series of 41 permanent plots was established in 27 wetlands to monitor vegetation change through time and to provide a mechanism to assess the effectiveness of conservation management activities carried out in the Lake Muir-Unicup catchment. This catchment is situated in the 600 – 800 mm rainfall zone and wide-scale plantings of eucalypt plantations for fiber production was believed to provide an economically feasible way to control rising water tables. This paper reports on the changes in wetland vegetation for the five years commencing in 1997.

Methods

Vegetation cover was recorded in 41 quadrats located in 27 wetlands in October 1997. Most were resurveyed in October 2002, however five quadrats (from three wetlands) could not be accessed at that time and were instead resurveyed in March 2003 (Fig. 1). Each quadrat was 5 m x 10 m with corners marked by steel star bars or droppers. Lists were compiled of all vascular species recorded in each quadrat and a percentage cover class was visually estimated for each species (<2, 2–10, 10–30, 30–70, >70%). In basin wetlands plots were laid out with their long axis parallel to the shoreline. Between one and three plots were established in different vegetation zones at each wetland. Where multiple quadrats were used, quadrats were placed in parallel along the littoral gradient. In all, five broad wetland types were sampled (*Baumea articulata* basin wetlands; flats and riparian zones dominated by *Baumea juncea;* swamps and flats with understorey dominated by *Lepidosperma longitudinale;* other wet flats; and one seasonally inundated claypan). The position of each quadrat was fixed with a GPS unit.

To test whether a significant change in vegetation cover of the quadrats had occurred over the five years a similarity matrix using midpoint cover values was constructed using Bray-Curtis similarity coefficients with data from all quadrats at both sampling times. This matrix was analyzed using the non parametric ANOSIM routine (Primer v5.2.8 Clark & Gorley 2001) which tests for differences between rank similarities of quadrats between years using a permutation test.

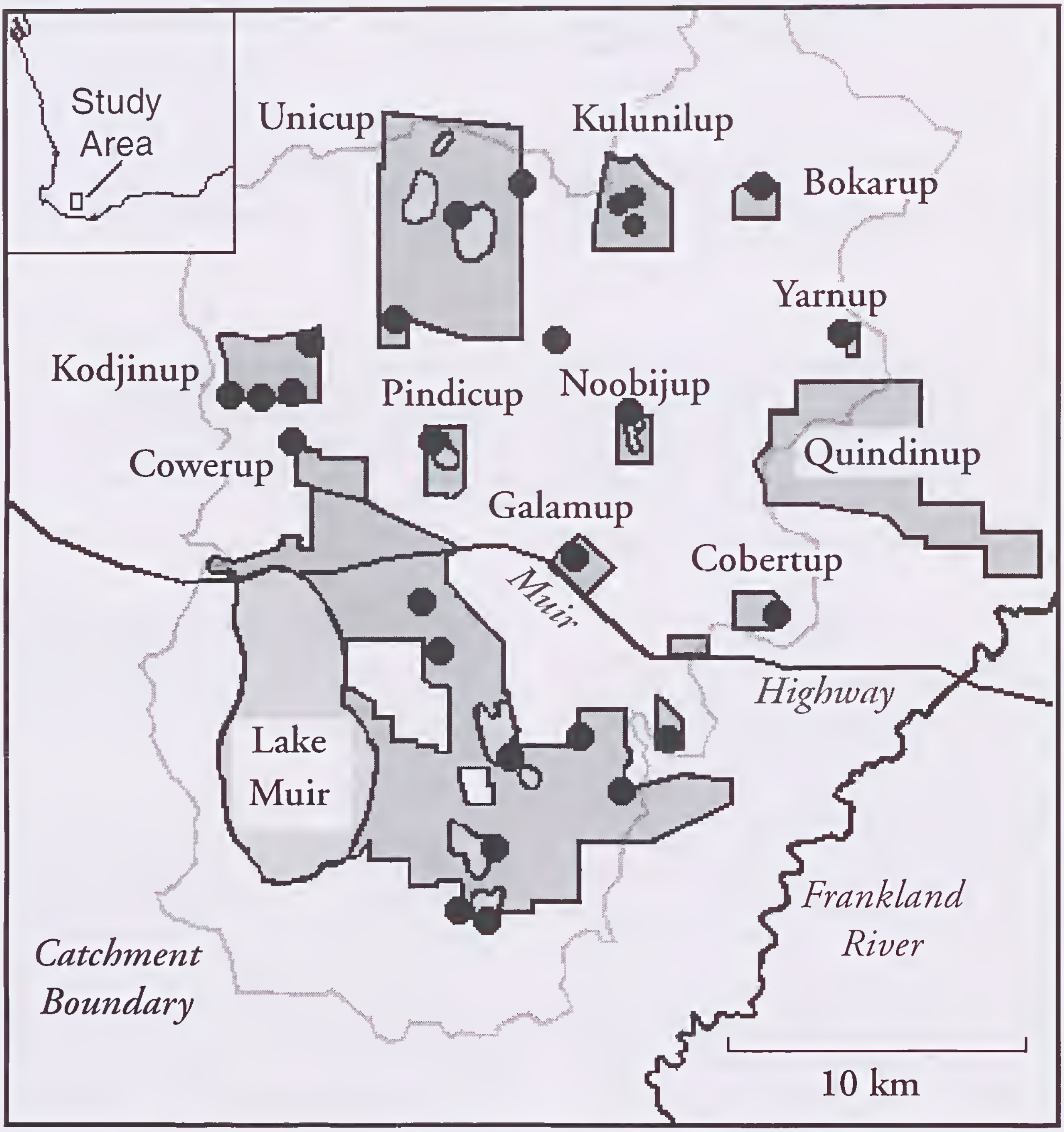

Figure 1. Location of the 27 wetlands (black dots) containing the 41 monitoring quadrats in the Lake Muir-Unicup catchment (light grey line). Nature Reserves occurring in the catchment are also shown.

Differences were further examined using two dimensional non-metric multidimensional scaling ordination (MDS in Primer v5.2.8) of the complete dataset and computing the distance quadrats moved in ordination space over the five year period.

At several of the wetlands in the Lake Muir-Unicup catchment, regular measurements are taken of water depth and water chemistry as part of the Department of Conservation and Land Management's long term wetland monitoring project begun in 1978 (Lane & Munro 1981).

Results

The five broad wetland types sampled were closely correlated with geomorphological position and floristic composition (N Gibson, unpublished data). Of these the *Baumea articulata* basin wetlands were very species poor and the flats and riparian zones dominated by *Baumea juncea* were less floristically variable than other wetland types (Fig. 2a).

The sample statistic from the ANOSIM analysis was -0.02 which was not significant (P = 0.97) indicating that

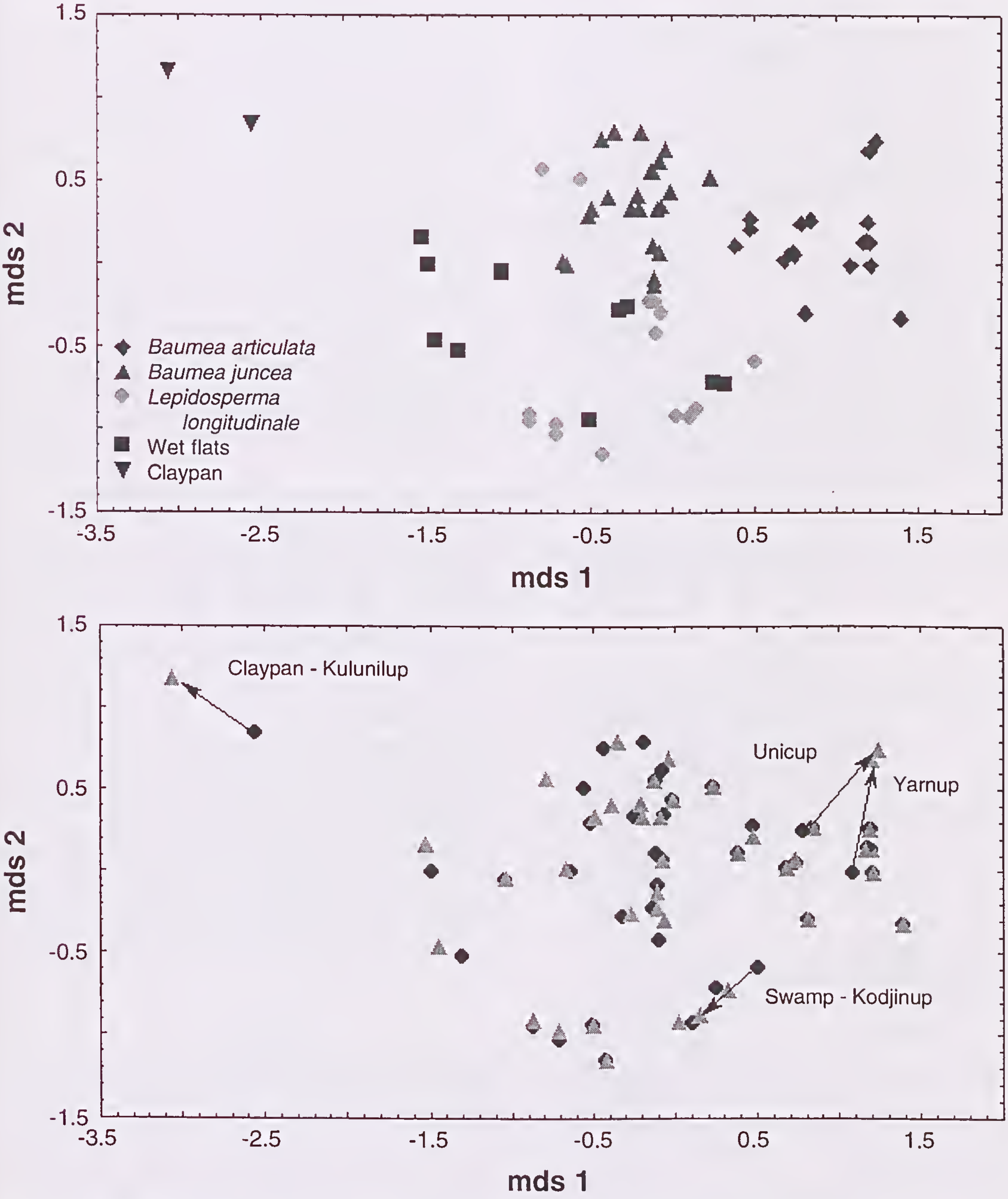

Figure 2. (a) Ordination showing five broad wetland types: *Baumea articulata* basin wetlands, flats and riparian zones dominated by *Baumea juncea*, swamps and flats with understorey dominated by *Lepidosperma longitudinale*, other wet flats, and claypans. (b) Non-metric multidimensional scaling ordination of the 41 quadrats in 1997 (diamonds) and 2002 (triangles) based on cover abundance data. The four quadrats that showed large movement in ordination space are indicated by an arrow.

there was no significant change in species abundance as a whole in the 41 quadrats over the five year period. A plot of the two dimensional ordination coded by year shows little or no movement for most quadrats in ordination space consistent with the ANOSIM results.

When the change in distance in ordination space for individual quadrats was calculated four quadrats showed large movement (Fig. 2b). Two of these quadrats were from species-poor *Baumea articulata* basin wetlands, the third from a *Melaleuca* swamp and

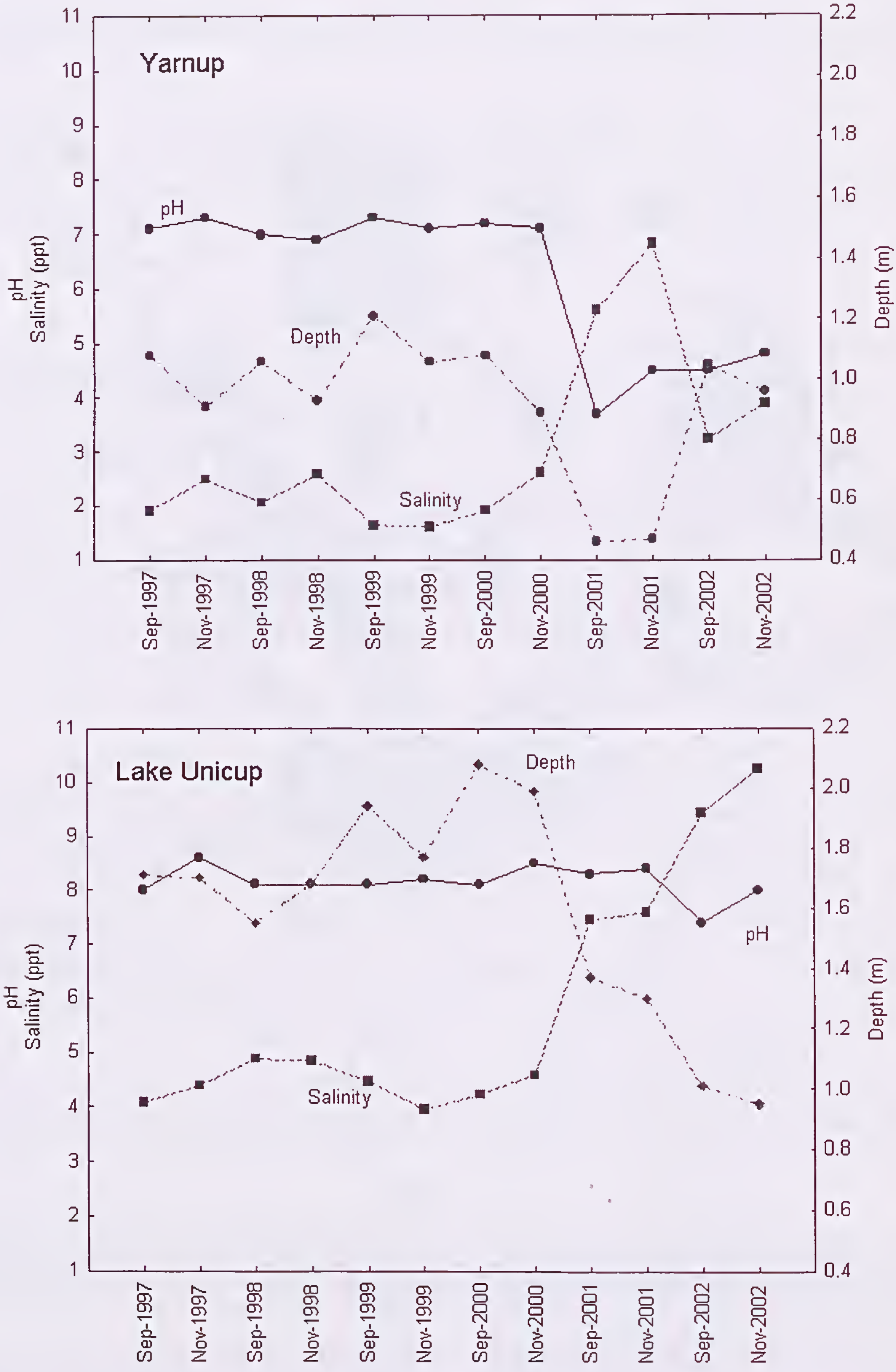

Figure 3. Changes in water pH, salinity and depth over the period 1997 to 2002. Water chemistry and depth were recorded twice yearly in September and November. (a) Yarnup; (b) Lake Unicup.

the fourth from a seasonally inundated claypan.

The two quadrats from species-poor *Baumea articulata* wetlands (Yarnup and Unicup) had a major collapse of the dominant species (the cover abundance scores of *B. articulata* changed from 30–70% to 2–10%). The Yarnup quadrat was immediately adjacent to the depth gauge while the Unicup quadrat was 100 m to the north of the depth gauge.

Water depth and pH of Yarnup Swamp were markedly lower in 2001 than in previous years and pH remained low in 2002 even after the return to more normal water depths (Fig. 3a). Similarly Yarnup's salinity was markedly higher in 2001 than in previous years and was also higher than usual in 2002 despite an increase in water depth. This wetland has a long term (1980–2002) trend of increasing salinity (JAK Lane, unpublished data). There was a marked decline in water depth – and increase in salinity – of Lake Unicup in 2001 and 2002 (Fig. 3b), however lake water pH did not change significantly.

The third site to show marked change over the monitoring period was a *Melaleuca* swamp in Kodjinup Nature Reserve. Here in 1997 the understorey was dominated by *Lepidosperma longitudinale* (30–70% cover) and *Baumea articulata* (10–30% cover) but by 2002 the *B. articulata* had almost disappeared. Only this single species showed a change in abundance at this quadrat. It is unclear whether this change represents gradual compositional shift of the swamp or an abrupt change of state since no water depth or water chemistry data are available.

The final quadrat that showed large movement in the ordination scores between 1997 and 2002 was on a seasonally inundated claypan in Kulunilup Nature Reserve. This claypan was dominated by *Apodasmia ceramophila* and these flats are characterized by the recruitment of a series of annual taxa as the claypan dries (N Gibson, unpublished data). The change noted at this quadrat is likely to have resulted from the claypan being sampled at different drying and floristic stages in October 2002 compared with October 1997. It does not represent habitat deterioration.

Discussion

The results of this monitoring are initially encouraging in relation to the maintenance of the biodiversity values of the wetlands in the Lake Muir-Unicup catchment. Only four of the 27 wetlands sampled showed obvious change over the study period. Two of these wetlands are known to have undergone significant changes in water quantity and / or quality during the period of monitoring. However, the lag period between land clearance and impact, and between restoration of perennial cover and improvement in ground water quality and depth, are known to be significant, perhaps being in the order of decades (National Land and Water Resources Audit 2001). Hence, results from any single monitoring interval need to be interpreted carefully.

More worrying in relation to the Lake Muir-Unicup catchment was the appearance of new saline springs both high and low in the landscape over the period 1997 – 2002 which were not related to surface drainage nor known hydrological source areas (R. Hearn, 2002, CALM, personal communication). These springs have appeared in upland areas in Unicup Nature Reserve, and in low lying areas of Kulunilup and Bokarup Nature Reserves but are not associated with the basin wetlands of these reserves.

The appearance of these springs suggests that current ground water levels are not yet in equilibrium and that the hydrological system is complex given that saline influences are not initially seen in basin wetlands where ground water intersection may have been first expected.

Detailed hydrological investigations are presently underway to identify recharge and discharge areas which will allow effective ground water management strategies to be developed (R. Hearn, 2003, CALM, personal communication). The three affected wetlands urgently need ground water management programs.

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Flora and vegetation of the Eastern Goldfields Ranges: Part 6. Mt Manning Range

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Abstract

This study of the flora and plant communities of the Mt Manning greenstone belt (some 100 km N of Koolyanobbing) recorded a total flora of 238 taxa, of which 234 were native and four were introduced. The species list is poorer than reported for previously studied ranges and shows a compositional shift consistent with the more semi-arid nature of the climate. The most common life-forms were shrubs 50% and annual herbs 23.5%. No taxa were found to be endemic to the greenstone belt. Seven community types were defined from 54 quadrats established along the range system. These communities types were strongly correlated with edaphic factors, and are compositionally distinct from those of nearby ranges to the south. The vegetation of the Mt Manning Range, like that of the Helena & Aurora Range to the south and Die Hardy Range to the west, is very poorly conserved. The results of the current survey support previous recommendations for the inclusion of the Mt Manning greenstone belt into the Nature Reserve.

Keywords: flora, vegetation, Goldfields, Mt Manning Range, Western Australia, greenstone

Introduction

The Mt Manning greenstone belt extends some 30 km from the Mt Manning Range north to the Evanston-Menzies Road, about 100 km north of Koolyanobbing. It consists of ca a 1 km-thick sequence of variously metamorphosed basalt overlain by chert and banded ironstone, which in turn is overlain by high-Mg basalt and minor gabbro separated by banded ironstone (Greenfield 2001). These belts are a common landform of the Eastern Goldfields and incorporate most of the mineralization. As a consequence, they have been heavily exploited for mineral exploration and mining for over 100 years. Despite this, a detailed knowledge of the flora and vegetation of individual ranges is still lacking, although broad scale structural vegetation mapping (Beard 1972) and regional surveys (Keighery *et al.*1995) are available.

This paper continues a this series of papers that report on detailed floristic studies on some of these ranges, to address this deficiency (Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2001a,b). The Mt Manning greenstone belt is the most arid system yet studied, and provides contrast to the biogeographic patterns reported from other range systems.

Study Locality

The study area lies ca 100 km north of Koolyanobbing and covers all of the Mt Manning greenstone belt (Fig 1; Greenfield 2001). The belt runs north-south and is ca 6 km wide but quickly narrows to less than 2 km. The geology of the study area has been mapped and described in detail in the Lake Giles and Bungalbin 1: 100000 sheets (Greenfield 2001, Chen & Wyche 2001) following earlier regional studies of Walker & Blight (1983). The lenticular greenstone belts of this region are believed to be 3000 My old and to have subsequently undergone multi-staged metamorphism that peaked with the major granitiod intrusion between 2710 and 2670 My ago. These ancient rocks have weathered into gently undulating plains and broad valleys covered by Tertiary soils (< 65 My old). These soils may develop in situ from the weathering of laterite duricrusts, or represent depositional soils derived from the ancient rocks or the Tertiary laterization (Greenfield 2001). The net result is a very subdued landscape except for the highly resistant banded ironstones which form a series of abrupt rocky outcrops.

The climate of the region is warm dry mediterranean with warm winters and hot summers. Mean annual rainfall at Diemals Station (ca 45 km NW of the range) is 275 mm, with moderate seasonal variation over the 23 years of record (1970-1994; decile 1, 157 mm; decile 9, 436 mm) Most rain falls in winter generally associated with frontal activity from April through August. Summer falls are highly erratic and result from thunderstorms. Heaviest falls (to 127 mm) are associated with rain bearing depressions forming from tropical depressions (Milewski & Hall 1995; Bureau of Meteorology 2004). The temperature data from Diemals show mean maximum temperatures is highest in January (36 °C) with November through March all recording mean annual temperatures above 30 °C. Lowest mean minimum temperatures of 4 °C are recorded in July. The highest daily maximum temperature recorded was 46.5 °C with the lowest being –4.6 °C. On average there are 15.9 days a year over 40 °C and 67.2 days above 35 °C, with 11.1 days per year with the minimum below freezing (Bureau of Meteorology 2004).

The Mt Manning Range lies in the South Western

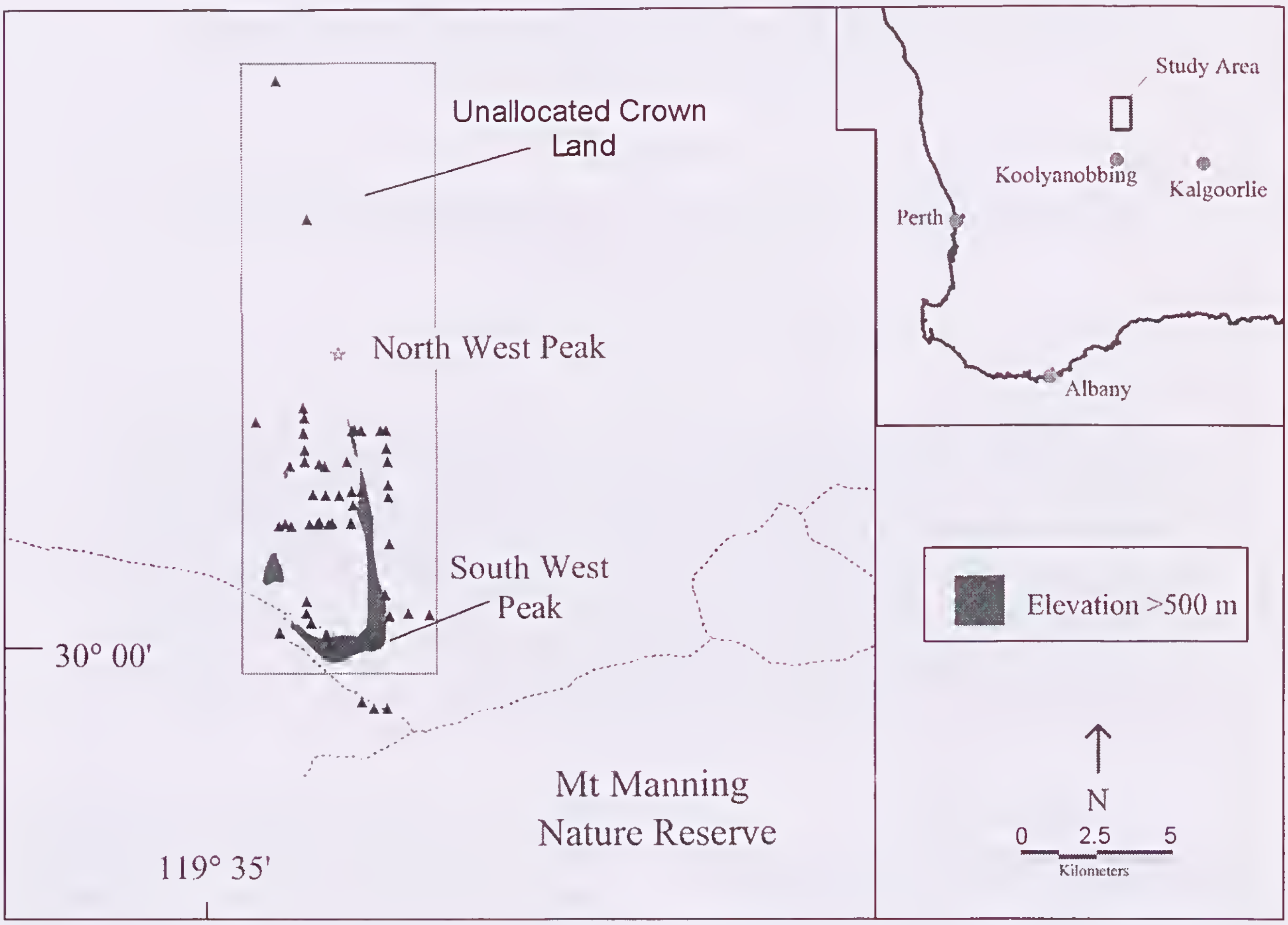

Figure 1. Location of the study area and distribution the 54 quadrats along the Mt Manning Range (solid triangles). Most of the uplands (and the quadrats sampled) fall in an enclave of Unallocated Crown Land within the Mt Manning Nature Reserve.

Interzone close to the border with the Murchison botanical region (Beard 1990). The Interzone is generally dominated by eucalypt woodlands and shrublands on yellow sandplains and it marks the transition in vegetation from the species-rich south west to the more arid communities of the desert regions. The Murchison region is dominated by mulga (*Acacia aneura*) low woodlands.

Beard (1972) described the major structural formations of the Jackson 1:250 000 sheet which lies immediately south of the Mt Manning Range. He consideres the Die Hardy vegetation system on the northern edge of that map sheet to be similar to that occurring on the banded ironstones of Mt Jackson and Koolyanobbing Range, but slightly different due to its lower rainfall. *Brachychiton gregorii* and *Dryandra arborea* are occasional trees on the range crest, with the northern slopes dominated by open scrubs of *Acacia aneura, A. linophylla, A. acuminata, A. tetragonophylla* and *Dodonaea* sp. The southern slopes support dense thickets of *Allocasuarina acutivalvis* and *A. campestris* with some acacias and eucalypts.

Keighery *et al.* (1995) ascribe the vegetation of the Mt Manning Range to this vegetation system. They identify 30 major structural vegetation units as occurring along the range. The ridges of the range support five structural units; *Acacia aneura* tall shrubland, *Eucalyptus ebbanoensis* mallee, *Acacia quadrimarginea* tall shrubland, *Dryandra arborea* tall shrubland, and *Allocasuarina acutivalvis* tall shrubland. The *E. ebbanoensis* mallee is a stunted version of the vegetation of the lower slopes. The two *Acacia* shrublands have similar composition but differing dominance and the *Dryandra* shrubland occupies lateritic patches on the ridge crests. Pure *Acacia aneura* low woodlands occur on lower slopes on deep colluvial soils while the valleys are dominated by *Eucalyptus salubris* and/or *E. salmonophloia* woodland or by *Casuarina pauper* (syn *C. cristata*) low woodland around the base of the Mt Manning Range and on small rises of greenstone on the plain. The surrounding sandplain is dominated by *Eucalyptus formanii* over *Plectrachne rigidissima*.

The aim of the present work was to undertake a detailed floristic survey of the Mt Manning greenstone belt. This involved the compilation of a detailed flora list, and the description of the vegetation patterning of the area based on a series of permanently located quadrats.

Methods

Fifty-four 20 m x 20 m quadrats were established on Mt Manning Range, side slopes and outwash plains surrounding the range (Fig 1). These quadrats attempted to cover the major geographical, geomorphological and floristic variation found in the study area. Care was taken to locate quadrats in the least disturbed vegetation available in the area being sampled. All vascular plants were recorded within each quadrat. Quadrats were permanently marked with four steel fence droppers and their positions determined using a GPS unit. Twenty-four soil samples from the upper 10 cm were collected from each quadrat. These were bulked and analyzed for electrical conductivity, pH, total N, total P, available K (McArthur 1991).

Quadrats were sampled in early November 1995. Data on topographical position, slope, aspect, percentage litter, percentage bare ground, percentage surface rock (bedrock and surficial deposits) and vegetation structure were collected from each quadrat. Topographical position was scored on a subjective six point scale; ridge tops = 1, upper slopes = 2, midslopes = 3, lower slopes = 4, valley flats =5, small rise in valley =6. Slope was scored on a one to three scale from flat to medium, to steep. Aspect was recorded as one of 16 cardinal directions. Altitude was taken from 1:100000 series topographical map to nearest 10 m. Vegetation structure was recorded using Muir's (1977) classification.

Quadrats were classified according to similarities in species composition. In these analyses only perennial species were used to facilitate comparisons with classifications from other ranges (Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2001a,b). The quadrat and species classifications undertaken used the Czekanowski similarity coefficient and "unweighted pair-group mean average" fusion method (UPGMA module in PATN, Belbin 1995, beta value -0.1, Sneath & Sokal, 1973). Semi-strong hybrid (SSH in PATN) ordination of the quadrat data was undertaken to show spatial relationships between quadrat groups (here referred to as community types) and to elucidate possible environmental correlates with the classification (Belbin 1991). Methods of Dufrene & Legendre (1997) were used to determine best indicator taxa for each group (from PC-ORD v 4.24, McCune & Mefford 1999).

Climate estimates (mean annual temperature, annual temperature range, mean annual rainfall, rainfall coefficient of variation) were obtained from BIOCLIM (Busby 1986), a prediction system that uses mathematical surfaces fitted to long term climate data. Relationships among and between physical site parameters and climate estimates were examined using Spearman rank correlation coefficient. To reduce the probability of type I errors given the number of intercorrelations, significance differences were reported at a level of $P<0.01$. Vectors for the physical site parameters, latitude, altitude and climatic estimates were fitted to the ordination along axes of highest correlation using the principal axis correlation routine (also known as rotational correlation analysis) in the PATN package (Belbin 1995). Statistical significance of these vectors was determined using random permutations of the values of the variable among sites (Faith & Norris 1989). Statistical relationships between quadrat groups for physical site parameters and climate estimates were tested using Kruskal-Wallis non-parametric analysis of variance (Siegel 1956).

Nomenclature generally follows Paczkowska & Chapman (2000). Voucher specimens have been be lodged in the Western Australian Herbarium. Introduced taxa are indicated by a "*".

Results

Flora

A total of 238 taxa (species, subspecies, varieties) were recorded from the Mt Manning greenstone belt (Appendix 1). The flora list was compiled from taxa found in the 54 quadrats or the adjacent area and from collections of the Western Australian Herbarium. Of these 238 taxa, 234 are native and four are weeds. Sampling was undertaken in the first week of November 1995 and although good rains had fallen in winter and spring of 1995, the annuals and geophytes were largely finished and further additions could be expected to the flora list. The best represented families were the Asteraceae (37 native taxa and 2 introduced taxa), Myrtaceae (32 taxa), Chenopodiaceae (13 taxa), Poaceae (12 native taxa and 2 introduced taxa) Myoporaceae (11 taxa), and Mimosaceae (10 taxa). This pattern is typical of the flora in changeover zone between the of the South Western Botanical Province and the Eremaean (Gibson *et al.* 2000). The most common genera were *Eucalyptus* (17 taxa), *Eremophila* (11 taxa) and *Acacia* (10 taxa). Most common life-forms were shrubs 50%, annual herb 23.5%, perennial herbs 5.5%, mallee 5.0%, trees 4.6% and perennial grasses 4.2%. These six life-forms accounted for over 92% of taxa recorded.

Six taxa of conservation significance (Atkins 2001) were recorded (*Calytrix creswellii, Daviesia purpurascens, Eremophila* sp (GJ Keighery 4372), *Eucalyptus formanii, Grevillea erectiloba,* and *Grevillea georgeana*). Of these *Eremophila* sp (GJ Keighery 4372) and *Calytrix creswellii* are the most poorly known, being represented by only 5 and 15 collections respectively in the Western Australian Herbarium. All six taxa with the exception of *Daviesia purpurascens* have a geographic range of ca 200 km and can be considered regional endemics of the greenstone and banded ironstone ranges (*Eremophila* sp (GJ Keighery 4372), *Grevillea erectiloba, Grevillea georgeana*) or the surrounding sandplain (*Calytrix creswellii, Eucalyptus formanii*), although the latter two taxa do also occur on the lower slopes or outwash plains of the Mt Manning Range.

Vegetation

Only plant material that could be identified to species or subspecies level was included in the analysis (ca 95% of records). In the 54 quadrats established on the Mt Manning Range, 197 taxa were recorded of which 142 were perennial. Fifty-five perennials occurred at only one quadrat. Preliminary analyses showed these singletons had no effect on the community classification and were therefore not considered further. As a result the final data set consisted of 87 perennial taxa in 54 quadrats. Species richness ranged from five to 23 taxa per quadrat, with individual taxa occurring in between two and 38 of the 54 quadrats.

The 54 quadrats were divided into two primary groups, the first group (types 1-5) containing quadrats with skeletal soils over banded ironstone or weathered yellow sand on banded ironstone or laterite, the second group (types 6 & 7) containing quadrats on greenstone or colluvial soils (Fig 2).

- Community type 1 were species poor quadrats that

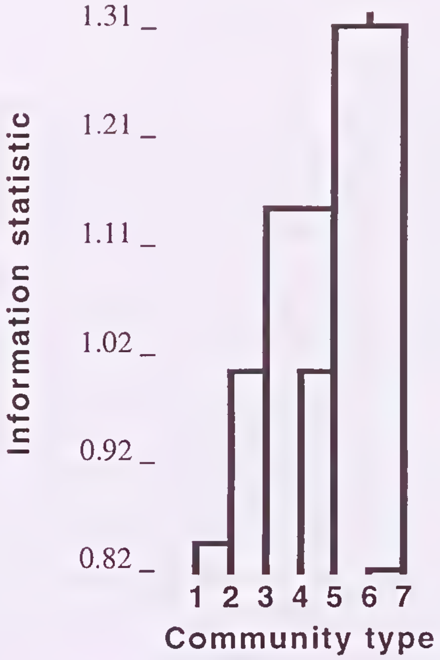

Figure 2. Dendrogram of 7 group level classification of 54 quadrats established along the Mt Manning greenstone belt.

generally occurred on massive banded ironstone near the crest of the range. Species richness was low (mean 10.5 taxa plot^{-1}) with only some taxa in species groups A and F (Appendix 2) being consistently represented. Best indicator species for this group were the rock fern (*Cheilanthes austrotenuifolia*), *Calycopeplus paucifolius*, *Austrostipa trichophylla*, and *Eremophila clarkei*. Other constant species to this group included the perennial grass *Amphipogon strictus*. One quadrat in this group occurred on massive greenstone on a small rise near the base of the range.

- Community type 2 occurs on the lower flanks of the ranges on somewhat deeper soils. This community type is generally dominated or co-dominated by *Eucalyptus ebbanoensis*, *Acacia ramulosa*, *A. aneura*, *A. quadrimarginea* and/or at the foot of the range by *Callitris glaucophylla*. Indicator taxa include *Callitris glaucophylla*, *Prostanthera althoferi* subsp *althoferi*. Species groups G and H are largely restricted to this community type but at low constancy levels (Appendix 2). Species group A is also well represented, as is *Eremophila latrobei* subsp *latrobei*. Average species richness was 12.7 taxa plot^{-1}.
- Around the base of the range and on some upland units, a characteristic yellow sand unit develops over laterite. Community type 3 occurs on this unit and is characterized by high constancy of taxa in species group F, half of which are indicator species. Typical co-dominant indicators include, *Allocasuarina acutivalvis*, *Melaleuca nematophylla* and *Acacia quadrimarginea*. Typical shrub indicators include *Baeckea elderiana*, *Hibbertia rostellata*, *Grevillea obliquistigma*, *Phebalium canaliculatum*, *Grevillea paradoxa* and *G. georgeana* (Appendix 2). Average species richness is high at 14.5 taxa plot^{-1}. This community is most common around the base of the range but does occur where ever the laterite sheet remains.
- Community type 4 occurs on eroding breakaways which are dominated by *Eucalyptus capillosa* subsp *capillosa*. This landform is very restricted at the Mt Manning Range; it is more common on the banded ironstones of the Helena and Aurora Range and the Yendilberin Hills to the south (Gibson *et al.* 1997; Gibson & Lyons 2001b).
- Community type 5 occurred at a single quadrat on sandy alluvial soils in a narrow drainage line at the base of the range. Species richness was low with only eight perennial species being recorded, three of which were only recorded at this quadrat. This quadrat was dominated by *Eucalyptus formanii*; it may represent either a depauperate example of community type 2 or be more representative of the surrounding sandplain that were not sampled in this study (Keighery *et al.* 1995).
- Community types 6 and 7 appear to represent community types on the more fertile soils lower in the landscape. Taxa in species group A are most faithful to these two communities.
- Community type 6 are eucalypt mallees and woodlands which are found on the lower slopes, valley and small rises in the valleys. These quadrats are generally dominated by *Eucalyptus griffithsii* and/or *E. ebbanoensis* or occasionally by *Casuarina pauper*. This community differs from community type 7 by the general lack of chenopods (Appendix 2). Best indicator taxa of this community included *Eucalyptus griffithsii*, *Olearia muelleri*, *Acacia tetragonophylla*, *Ptilotus obovatus* and *Acacia erinacea*. Average species richness was high at 16.9 taxa plot^{-1}.
- The final community type (type 7) is the chenopod rich eucalypt woodlands of the valleys and small rises. Common dominants include *Eucalyptus salubris* and occasionally *Casuarina pauper*. Indicator taxa were largely chenopods (Appendix 2). Average species richness was again high at 14.5 taxa plot^{-1}.

Physical Correlates

Soil parameters showed high levels of intercorrelation, as did the site parameters and the climate parameters. Total P was not correlated with any other soil parameter except for total N, while total N was not correlated with pH (Table 1). All other soil parameters were intercorrelated. Of the site parameters only topographic position showed no intercorrelation while slope, aspect, percentage rock, percentage litter and percentage bare ground were all highly intercorrelated. Altitude, latitude and the four climate parameters also showed a significant degree of intercorrelation. A much lower degree of intercorrelation was evident between these three different types (soil, site and climate) of parameters (Table 1).

Table 1

Matrix of Spearman rank correlation coefficients between site physical parameters and climate estimates. Only correlation significant at $P < 0.01$ shown. (Climate parameter codes: Tann, mean annual temperature; Tar, annual temperature range; Rann, mean annual rainfall; Rcv, rainfall coefficient of variation.)

	EC	pH	N	P	K	Position	Slope	Aspect	% rock	% litter	% bare	altitude	latitude	Tann	Tar	Rann	Rcv
EC	1.000																
pH	0.558	1.000															
N	0.689		1.000														
P			0.612	1.000													
K	0.706	0.765	0.576	0.441	1.000												
Position	0.364	0.620			0.485	1.000											
Slope							1.000										
Aspect							0.604	1.000									
% rock			0.449				0.473	0.451	1.000								
% litter							-0.477	-0.433	-0.532	1.000							
% bare			-0.428				-0.532	-0.452	-0.800	0.353	1.000						
Altitude		-0.535				-0.445						1.000					
Latitude													1.000				
Tann		0.465										-0.659	0.455	1.000			
Tar				-0.404									0.875		1.000		
Rann												0.738		-0.828		1.000	
Rcv																-0.362	1.000

Table 2

Plant community mean values for soil, site and climate parameters. Differences between means of groups 1, 2, 3, 6,and 7 tested using Kruskal-Wallis non-parametric analysis of variance. Mean species richness and number of quadrats given for comparison. (* indicates P<0.05, ** indicates P<0.01, *** indicates P<0.001.) Climate parameter codes: Tann, mean annual temperature; Tar, annual temperature range; Rann, mean annual rainfall; Rcv, rainfall coefficient of variation.

				Community type			
	1	2	3	4	5	6	7
EC**	6.3	2.7	2.8	58.0	2.0	6.0	9.4
pH***	5.1	4.7	4.6	4.4	5.5	6.1	6.8
N*	0.125	0.054	0.057	0.090	0.034	0.070	0.082
P	230.8	145.1	98.5	180.0	88.0	131.5	165.7
K***	155.0	149.6	83.8	160.0	91.0	220.5	368.6
Position	2.5	4.7	3.1	4.0	5.0	5.2	5.1
Slope	2.3	1.5	1.4	2.0	2.0	1.7	1.4
Aspect	5.5	2.1	3.3	4.0	4.0	3.1	2.1
% rock**	85.0	22.0	53.6	90.0	10.0	59.5	30.7
% litter*	10.0	31.5	27.7	10.0	10.0	26.0	42.9
% bare**	0.0	33.0	19.1	0.0	10.0	13.0	25.7
Altitude**	560	484	485	480	450	475	471
Latitude	-29.9700	-29.9673	-29.9250	-29.9851	-29.9961	-29.9551	-29.9693
Tann**	18.8	19.1	19.2	19.1	19.2	19.2	19.2
Tar	30.2	30.1	30.2	30.1	30.1	30.2	30.1
Rann*	254.5	247.1	246.6	247.0	244.0	246.2	246.3
Rcv	33.0	33.0	33.1	32.9	33.2	33.0	33.0
Richness	10.5	12.7	14.5	7.0	5.0	16.9	15.4
No quadrats	4	10	11	1	1	20	7

As community types 4 and 5 were only represented by single quadrats, they were excluded from the statistical analysis of environmental differences. Significant differences were found between mean values for three of the four soil parameters, three of the six site parameters and three of the six climate parameters for community types 1, 2, 3, 6 and 7 (Table 2). Community type 1 showed a high percentage of exposed rock and occurred at higher altitudes with a higher estimated rainfall than other community types. The soils of this community were high in total N and had a higher pH and EC than community types 2 and 3 which occurred on deeper more acid sands. Community types 2 and 3 were differentiated primarily on available K, percentage surface rock and percentage bare ground. The single quadrat that sampled a breakaway (type 4) showed very high values of EC probably related to erosion of the freshly exposed clays beneath the duricrust. The soils of community types 6 and 7 were close to neutral, showed high levels of available K and intermediate levels of total N and occurred at lower altitude than types 1 to 3. The chenopod rich community type 7 had the highest pH, and highest levels of available K recorded as well as the best developed litter layer (Table 2).

The edaphic differences between community types are also reflected in the ordination (stress 0.18 for the three dimensional solution) on which the highest correlated environmental vectors have been plotted (Fig 3). Community types 6 and 7 typical of the lower slopes and outwash flats occur in the lower left quadrant. The skeletal higher nutrient soils of the top of the range (type 1) occur in the middle right of the figure while the nutrient poor sandy soils (of types 2 and 3) in the upper right of the figure. The outlying nature of community type 5 can be seen while community type 4 is very different from the others in the third dimension (not shown). In addition to edaphic factors, altitude and rainfall, topographic position and percentage litter cover were significantly correlated with the quadrats in ordination space (Fig 3).

Discussion

The total of 238 taxa that we recorded on the Mt Manning Range compares with 293 taxa recorded by Keighery *et al.* (1995) for the sandplains of Mt Manning Range Nature Reserve, in addition to the range. The total for the range is low compared with the list for the Helena and Aurora Range (324 taxa), and this probably reflects in part the sampling of the Mt Manning Range later in the season when many of the annuals and geophytes were not as apparent (Gibson *et al.* 1997). However the flora list for the range is also lower than those for the Bremer Range (267 taxa) and the Parker Range (254 taxa), which were also sampled in a very poor year for annuals and geophytes (Gibson & Lyons 1998a,b). This low total species richness is also consistent with a decline in species richness along an increasing aridity gradient (Beard 1972). The Mt Manning Range lies just south of the boundary between the South Western Interzone and the Murchison botanical region. The Interzone is the change over zone between the species-rich South West and the more arid Eremaean zone.

Beard (1972) mapped the southern extreme of the Mt Manning Range as part of the Jackson vegetation system but later stated (Beard 1976) that the Mt Manning Range was probably similar to the vegetation of the Die Hardy system covering the banded ironstone formations of the

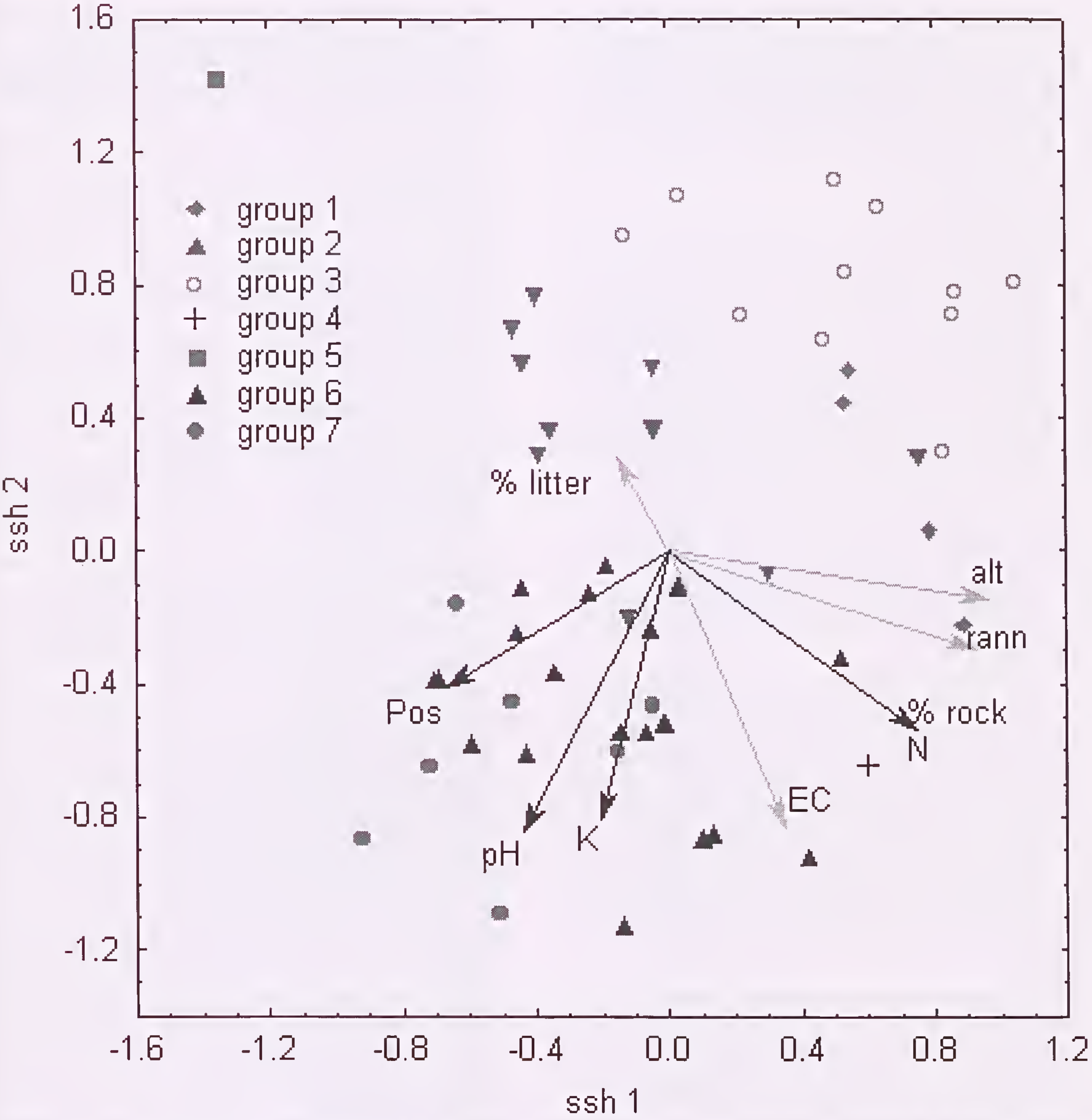

Figure 3. Ordination of the 54 quadrats coded by community type. Arrows show the direction of the best fit linear correlation environmental parameters; open arrows P<0.05, solid arrows P<0.001.

Die Hardy Range. Keighery *et al.* (1995) concurred that the vegetation of the Mt Manning Range area should be considered part of Beard's Die Hardy vegetation system. Further detailed survey work of the Die Hardy Range is needed to assess this.

The data suggest that floristic variation across the range is considerably less than structural variation described by Keighery *et al.* (1995). The present classifications allow the placement of the structural units described earlier to be set in a topography-soil context.

We were not able to relocate the *Dryandra arborea* shrubland on the top of Mt Manning Range described by Keighery *et al.* (1995) despite extensive searches in the region of South East Peak, the ridge to the west, and the more extensive ridge to the north. This community type, which is common on the massive ironstone tops of the Helena & Aurora Range (70 km to the south), must be localized in small patches on the Mt Manning Range. This decrease in the occurrence of this community type is likely to be associated with the decreasing rainfall (Beard 1972). *Dryandra arborea* was encountered twice off the range, on skeletal soils over decomposing granites and on deep yellow sands. Both populations occur on the gridline between North West Peak and the Evanston-Menzies road. These populations represent the northern limits of this species.

Keighery *et al.* (1995) listed *Neurachne* sp (GJK & JA 1951) as a common perennial grass of the *Eucalyptus ebbanoensis* woodlands of the lower slopes. This taxon was not recorded during the current survey. Common perennial grasses recorded included *Amphipogon strictus*, *Austrostipa trichophylla*, and *Austrostipa elegantissima*. The *Neurachne* may have been missed due to lateness of the survey. The distribution of this species on the range needs clarification.

A significant number of new populations of *Grevillea erectiloba* and *Grevillea georgeana* were located during the present survey. These species are of conservation concern (Atkins 2001). *Grevillea georgeana* generally occurs on massive banded ironstone while *G. erectiloba* generally occurs on yellow sands over laterites around the base of the range. Of the five regional endemics of the banded ironstones and associated soils of the Helena and Aurora 70 km to the south (Gibson *et al.*1997), *Grevillea erectiloba*, *Grevillea georgeana* and *Mirbelia* sp Helena & Aurora (BJL 2003) occur as far north as the Mt Manning Range.

The main section of the Mt Manning Range is in an enclave of Unallocated Crown Land within the Mt Manning Nature Reserve ("the doughnut reserve" Fig 1). So despite being surrounded by a Nature Reserve only a few hundred hectares of the vegetation of the Mt Manning greenstone belt is presently reserved (Greenfield 2001).

The present survey clearly shows that the ridge and slope communities are fundamentally different in composition from those reported for the Helena and Aurora Range (Gibson *et al.* 1997). The Helena and Aurora Range is also composed of massive banded ironstones of the same age (Chin & Smith 1983). The differences in vegetation and flora most likely reflect differences in present day climate, or past history during the arid periods of the Tertiary (Hopper 1979), or both. Previous studies have suggested that the vegetation of the range is most similar to that on the Die Hardy Range (Beard's Die Hardy vegetation system), this remains to be tested.

The vegetation of the Mt Manning Range like the vegetation of the Helena & Aurora and Die Hardy Ranges is very poorly conserved. Our work supports the recommendations of CALM (1994) and Keighery *et al.* (1995) that the Mt Manning Range should become part of the Mt Manning Nature Reserve.

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APPENDIX 1

Flora list for Mt Manning Range, includes all taxa from the sampling quadrats and adjacent areas and collections lodged in the Western Australian Herbarium from the range. Nomenclature generally follows Paczkowska and Chapman (2000), * indicates an introduced taxon.

- Adiantaceae
  - *Cheilanthes austrotenuifolia*
  - *Cheilanthes lasiophylla*
- Amaranthaceae
  - *Ptilotus aervoides*
  - *Ptilotus divaricatus*
  - *Ptilotus drummondii*
  - *Ptilotus exaltatus*
  - *Ptilotus gaudichaudii*
  - *Ptilotus holosericeus*
  - *Ptilotus leucocoma*
  - *Ptilotus obovatus*
- Anthericaceae
  - *Thysanotus patersonii*
  - *Thysanotus speckii*
- Apiaceae
  - *Daucus glochidiatus*
  - *Trachymene ornata*
- Apocynaceae
  - *Alyxia buxifolia*
- Asclepiadaceae
  - *Marsdenia australis*
  - *Rhyncharrhena linearis*
- Asteraceae
  - *Actinobole uliginosum*
  - *Asteridea athrixioides*
  - *Blennospora drummondii*
  - *Calotis hispidula*
  - *Calotis multicaulis*
  - *Cephalipterum drummondii*
  - *Chthonocephalus pseudevax*
  - *Erymophyllum ramosum* subsp *ramosum*
  - *Gilberta tenuifolia*
  - *Gilruthia osbornei*
  - *Gnephosis tenuissima*
  - **Hypochaeris glabra*
  - *Lawrencella rosea*
  - *Leucochrysum fitzgibbonii*
  - *Millotia* sp
  - *Olearia exiguifolia*
  - *Olearia humilis*
  - *Olearia muelleri*
  - *Olearia pimeleoides*
  - *Olearia stuartii*
  - *Olearia subspicata*
  - *Podolepis canescens*
  - *Podolepis capillaris*
  - *Podolepis lessonii*
  - *Podotheca angustifolia*
  - *Rhodanthe citrina*
  - *Rhodanthe laevis*
  - *Rhodanthe manglesii*
  - *Rhodanthe oppositifolia*
  - *Rhodanthe rubella*
  - *Rhodanthe stricta*
  - *Schoenia cassiniana*
  - *Senecio glossanthus*
  - **Sonchus oleraceus*
  - *Streptoglossa cylindriceps*
  - *Streptoglossa liatroides*
  - *Trichanthodium skirrophorum*
  - *Vittadinia humerata*
  - *Waitzia acuminata*
- Boraginaceae
  - *Halgania integerrima*
- Brassicaceae
  - *Stenopetalum filifolium*
  - *Stenopetalum pedicellare*
- Caesalpiniaceae
  - *Senna artemisioides* subsp *filifolia*
  - *Senna pleurocarpa* var *pleurocarpa*
- Campanulaceae
  - *Wahlenbergia tumidifructa*
- Casuarinaceae
  - *Allocasuarina acutivalvis*
  - *Allocasuarina campestris*
  - *Allocasuarina corniculata*
  - *Allocasuarina eriochlamys* subsp *eriochlamys*
  - *Allocasuarina helmsii*
  - *Casuarina pauper*
- Chenopodiaceae
  - *Atriplex nummularia*
  - *Atriplex vesicaria*
  - *Enchylaena tomentosa*
  - *Maireana georgei*
  - *Maireana pentatropis*
  - *Maireana radiata*
  - *Maireana trichoptera*
  - *Maireana triptera*
  - *Rhagodia drummondii*
  - *Sclerolaena densiflora*
  - *Sclerolaena diacantha*
  - *Sclerolaena fusiformis*
  - *Threlkeldia diffusa*
- Crassulaceae
  - *Crassula colorata*
- Cupressaceae
  - *Callitris glaucophylla*
- Cyperaceae
  - *Lepidosperma* sp
- Dasypogonaceae
  - *Xerolirion divaricata*
- Dilleniaceae
  - *Hibbertia rostellata*
  - *Hibbertia spicata*
- Droseraceae
  - *Drosera menziesii*
- Epacridaceae
  - *Leucopogon* sp Clyde Hill (MA Burgman 1207)
- Euphorbiaceae
  - *Calycopeplus paucifolius*
  - *Poranthera microphylla*
- Frankeniaceae
  - *Frankenia desertorum*
- Geraniaceae
  - *Erodium cygnorum*
- Goodeniaceae
  - *Brunonia australis*
  - *Dampiera juncea*
  - *Dampiera roycei*
  - *Goodenia berardiana*
  - *Goodenia occidentalis*
  - *Scaevola spinescens*
  - *Velleia hispida*
  - *Velleia rosea*
- Haloragaceae
  - *Glischrocaryon flavescens*
  - *Gonocarpus nodulosus*
  - *Haloragis gossei*
- Lamiaceae
  - *Lachnostachys coolgardiensis*
  - *Physopsis viscida*
  - *Prostanthera althoferi* subsp *althoferi*
  - *Prostanthera grylloana*
  - *Westringia cephalantha*
- Lauraceae
  - *Cassytha nodiflora*
- Lobeliaceae
  - *Lobelia heterophylla*
- Loganiaceae
  - *Phyllangium paradoxum*

- Loranthaceae
  - *Amyema gibberula*
  - *Amyema miquelii*
- Malvaceae
  - *Abutilon otocarpum*
  - *Abutilon oxycarpum*
  - *Lawrencia* sp
  - *Sida atrovirens*
  - *Sida calyxhymenia*
  - *Sida chrysocalyx*
- Mimosaceae
  - *Acacia acuminata*
  - *Acacia andrewsii*
  - *Acacia aneura*
  - *Acacia coolgardiensis* subsp *effusa*
  - *Acacia erinacea*
  - *Acacia kempeana*
  - *Acacia neurophylla*
  - *Acacia quadrimarginea*
  - *Acacia ramulosa*
  - *Acacia tetragonophylla*
- Myoporaceae
  - *Eremophila alternifolia*
  - *Eremophila clarkei*
  - *Eremophila decipiens*
  - *Eremophila glabra* subsp *glabra*
  - *Eremophila interstans*
  - *Eremophila ionantha*
  - *Eremophila latrobei* subsp *latrobei*
  - *Eremophila oldfieldii* subsp *angustifolia*
  - *Eremophila oppositifolia* subsp *oppositifolia*
  - *Eremophila scoparia*
  - *Eremophila* sp Mt Jackson (GJ Keighery 4372)
- Myrtaceae
  - *Aluta aspera* subsp *aspera*
  - *Baeckea elderiana*
  - *Calytrix creswellii*
  - *Calytrix divergens*
  - *Eucalyptus brachycorys*
  - *Eucalyptus capillosa* subsp *capillosa*
  - *Eucalyptus ebbanoensis* subsp *ebbanoensis*
  - *Eucalyptus ebbanoensis* subsp *glauciramula*
  - *Eucalyptus formanii*
  - *Eucalyptus grasbyi*
  - *Eucalyptus griffithsii*
  - *Eucalyptus kochii* subsp *amaryssia*
  - *Eucalyptus leptopoda* subsp *subluta*
  - *Eucalyptus longicornis*
  - *Eucalyptus loxophleba* subsp *lissophloia*
  - *Eucalyptus moderata*
  - *Eucalyptus oldfieldii*
  - *Eucalyptus oleosa* subsp *repleta*
  - *Eucalyptus salubris*
  - *Eucalyptus subangusta* subsp *subangusta*
  - *Eucalyptus yilgarnensis*
  - *Euryomyrtus maidenii*
  - *Homalocalyx thryptomenoides*
  - *Malleostemon roseus*
  - *Melaleuca acuminata*
  - *Melaleuca fulgens*
  - *Melaleuca leiocarpa*
  - *Melaleuca nematophylla*
  - *Melaleuca uncinata*
  - *Thryptomene kochii*
  - *Thryptomene urceolaris*
  - *Verticordia helmsii*
- Orchidaceae
  - *Oligochaetochilus pictus*
  - *Thelymitra* aff *macrophyllum*
- Papilionaceae
  - *Daviesia purpurascens*
  - *Mirbelia depressa*
  - *Mirbelia ramulosa*
  - *Mirbelia* sp Helena & Aurora (BJ Lepschi 2003)
- Phormiaceae
  - *Dianella revoluta*
- Pittosporaceae
  - *Bursaria occidentalis*
  - *Cheiranthera filifolia* var *filifolia*
- Plantaginaceae
  - *Plantago* aff *hispidula* (NG & KB 3179)
- Poaceae
  - *Amphipogon strictus*
  - *Aristida holathera*
  - *Austrodanthonia caespitosa*
  - *Austrostipa elegantissima*
  - *Austrostipa platychaeta*
  - *Austrostipa trichophylla*
  - *Bromus arenarius*
  - *Eragrostis dielsii*
  - *Monachather paradoxus*
  - *Neurachne* sp (GJK & JA 1951)
  - **Pentaschistis airoides*
  - *Triodia rigidissima*
  - *Triodia scariosa*
  - **Vulpia myuros*
- Portulacaceae
  - *Calandrinia eremaea*
  - *Calandrinia* sp Bungalbin (GJK& NG 1656)
- Proteaceae
  - *Dryandra arborea*
  - *Grevillea acuaria*
  - *Grevillea erectiloba*
  - *Grevillea georgeana*
  - *Grevillea nematophylla* subsp *nematophylla*
  - *Grevillea obliquistigma*
  - *Grevillea paradoxa*
  - *Hakea minyma*
- Rhamnaceae
  - *Stenanthemum stipulosum*
- Rubiaceae
  - *Psydrax suaveolens*
- Rutaceae
  - *Boronia coerulescens*
  - *Phebalium canaliculatum*
  - *Phebalium filifolium*
  - *Phebalium tuberculosum*
  - *Philotheca brucei* subsp *brucei*
  - *Philotheca tomentella*
- Santalaceae
  - *Exocarpos aphyllus*
  - *Santalum acuminatum*
  - *Santalum spicatum*
- Sapindaceae
  - *Dodonaea divaricata*
  - *Dodonaea lobulata*
  - *Dodonaea rigida*
  - *Dodonaea stenozyga*
  - *Dodonaea viscosa*
- Solanaceae
  - *Nicotiana occidentalis*
  - *Solanum cleistogamum*
  - *Solanum lasiophyllum*
  - *Solanum orbiculatum*
  - *Solanum plicatile*
- Stackhousiaceae
  - *Stackhousia intermedia*
- Sterculiaceae
  - *Brachychiton gregorii*
  - *Keraudrenia velutina* subsp *elliptica*
- Stylidiaceae
  - *Stylidium induratum*
  - *Stylidium limbatum*
  - *Stylidium repens*
  - *Stylidium yilgarnense*
- Zygophyllaceae
  - *Zygophyllum apiculatum*
  - *Zygophyllum eremaeum*
  - *Zygophyllum ovatum*

Appendix 2

Sorted two-way table of quadrats established on the Mt Manning greenstone belt showing species occurrence by community type. Quadrats appear as columns and species as rows. Taxa in bold are indicator species identified by INDVAL (Dufrene & Legendre 1997) at four group level (P < 0.05). Single quadrat groups (types 4 and 5) not considered. Statistical significance tested by randomization procedure.

	Community type						
	1	2	3	4	5	6	7
SPECIES GROUP A							
Acacia acuminata	**	* *	**			***** * * *	
Acacia ramulosa	*	********	*** ******			** **** *	*
Amphipogon strictus	****	**********	****** ****			***** **** *** **	
Thysanotus patersonii	**	**** *	***** *			*** *** *	*
Acacia erinacea				*		*** ** *******	***
Maireana trichoptera						* * ** *	***
Austrodanthonia caespitosa			*			* **** * *** * * **	* * *
Olearia muelleri						*************** **	* * *
Senna artemisioides subsp *filifolia*		* **** *				* ****** *** **	**
Austrostipa elegantissima	* *	* *** **	* *			********** * * **	*******
Austrostipa trichophylla	****	* *****				* ********* *******	* ****
Ptilotus obovatus	**	****				** *********** *****	** *
Scaevola spinescens		** * * *	* * *			** **** * * *** *	** *
Eucalyptus griffithsii		* *				* **** ******	
Maireana georgei		*				** * **** ** **	*****
Ptilotus gaudichaudii	*	* *	*			**** ** * * **	
Eremophila oppositifolia subsp *oppositifolia*		*		*		*** * ***	**
Eucalyptus ebbanoensis		**** *	*			* * ****	
Atriplex nummularia						****** *	* * **
Rhagodia drummondii						****** *	* *****
Sclerolaena diacantha						** *** *	* *****
Atriplex vesicaria						* * * *	*****
Eremophila scoparia						** ** **	** ***
Ptilotus exaltatus		**				** * **** *	* *****
Sclerolaena fusiformis		*				* *	******
SPECIES GROUP B							
Acacia tetragonophylla		* *				*** **** * ** **	*
Casuarina pauper						* * ** **	*
Exocarpos aphyllus						** * * ** *	*
Eremophila decipiens						* * * ***	*
Dodonaea lobulata		*				* *****	
Eremophila oldfieldii subsp *angustifolia*		*				* ** * ****	*
Alyxia buxifolia		*	* *	*		* ** * * ** *	
Eremophila interstans						** *	*
Eremophila sp Mt Jackson (GJ Keighery 4372)						* *	
Eucalyptus longicornis						**	*
Dodonaea rigida		*	*			*	
Santalum spicatum		*	* *			** * * **	
SPECIES GROUP C							
Allocasuarina campestris	*					*	
Dodonaea stenozyga						* *	
Eremophila glabra subsp *glabra*						* *	*
Ptilotus aervoides						***	* * *
SPECIES GROUP D							
Enchylaena tomentosa		*					*
Ptilotus divaricatus		*			*	*	*
Eucalyptus grasbyi		*					**
Eucalyptus salubris							****
Rhyncharrhena linearis	*		*			*	**
SPECIES GROUP E							
Austrostipa platychaeta						** **	
Threlkeldia diffusa				*		*	*
Eremophila ionantha						**	**
Maireana pentatropis						*	*

	Community type						
	1	2	3	4	5	6	7
Maireana radiata						*	** *
Eucalyptus oleosa subsp *repleta*						*	*
SPECIES GROUP F							
Acacia aneura	*	*** *	*				
Acacia quadrimarginea	*	*** ** *	** ******			*	
Eremophila latrobei subsp *latrobei*		*** *	*** *				
Allocasuarina acutivalvis	* *		** *******	*			
Baeckea elderiana			**********				
Melaleuca nematophylla	*		******				
Calycopeplus paucifolius	** *		** ****				
Grevillea paradoxa	*		* ******				
Leucopogon sp Clyde Hill (MA Burgman 1207)	*	*	******				
Hibbertia spicata	*		* *** *				
Prostanthera grylloana	*		* * ** *				
Grevillea obliquistigma			** ****		*		
Hibbertia rostellata			**** ** *				
Phebalium canaliculatum		**	***** * **				
Cheilanthes austrotenuifolia	****		****			*	
Philotheca brucei subsp brucei	**		* ****	*			
Grevillea georgeana			* * *				
Stylidium yilgarnense			**				
SPECIES GROUP G							
Acacia coolgardiensis subsp *effusa*		*	*				
Westringia cephalantha		* *				* * *	
Aluta aspera subsp *aspera*		**					
Callitris glaucophylla		***					
Ptilotus leucocoma		**					
Olearia pimeleoides	*	** ***	*				
Prostanthera althoferi subsp *althoferi*		* ****	*				
Monachather paradoxus		* ***	** *			*	
SPECIES GROUP H							
Mirbelia depressa		**					
Oligochaetochilus pictus		*		*			
Sida atrovirens		* *					
Sida calyxhymenia	*	*				**	
SPECIES GROUP I							
Eremophila clarkei	**	*	* *				
Eucalyptus formanii		*	* **		*		
Euryomyrtus maidenii		*	* **				
Phebalium tuberculosum		*	*		*		
Triodia rigidissima			*		*		

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Flora and vegetation of the Eastern Goldfields Ranges: Part 7. Middle and South Ironcap, Digger Rock and Hatter Hill

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Abstract

A study of the flora and plant communities of part of Forrestania greenstone belt between Middle Ironcap and Hatter Hill (some 80 km ESE of Hyden), recorded a total flora of 345 taxa of which 342 were native and three were introduced. Three species of threatened flora and 29 taxa being considered for listing were found. Ten species are considered to be endemic to the range and a further eight species are restricted to similar landforms within 100 km of the range. A new species of *Stenanthemum* is only known from two populations. Despite considerable mining and exploration activity in the area, the flora and vegetation remain poorly known. Thirty-eight quadrats were established along the range system and data from these quadrats were used to define four community types. Differences in these community types were strongly related to edaphic gradients. Very little of the Forrestania vegetation system is reserved and the results of this survey support recommendations for the establishment of nature reserves to conserve this vegetation system.

Keywords: flora, vegetation, Goldfields, Ironcap, Hatter Hill, Digger Rock, Western Australia, greenstone

Introduction

The Forrestania greenstone belt extends from Mt Holland south to Hatter Hill, a distance of some 70 km, and lies 80 km east of Hyden. This narrow greenstone belt is composed of an undulating plain of mafic and ultramafic lithologies and abrupt ridges of banded ironstones, and forms part of the western most greenstone series (Chin *et al.* 1984). These belts are common landforms of the Eastern Goldfields and have been heavily exploited for mineral exploration and mining for over 100 years. Despite this, a detailed knowledge of the flora and vegetation of individual ranges is still lacking although broad scale structural vegetation mapping (Beard 1972) and regional surveys are available (Newbey & Hnatiuk (1988).

The aim of this series of papers is to report on detailed floristic studies on some of these ranges to address this deficiency (Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2001a,b). This work has highlighted the high biodiversity values of these ranges as centres of endemism and restricted vegetation assemblages within the subdued landscapes of the eastern goldfields.

Study Locality

The study area lies ca 80 km ESE of Hyden and covers the section of the Forrestania greenstone belt between Middle Ironcap and Hatter Hill (Fig 1). The northern portion of this belt was burnt by a large, extremely hot, wildfire in summer of 1993 that consumed almost all vegetation between Mt Holland and Middle Ironcap. The northern section of the belt runs roughly north–south then swings north west–south east near South Ironcap.

The regional geology of the study area has been mapped and described in the Hyden 1: 250000 sheet (Chin *et al.* 1984) and the geology and landforms have also been summarized by Newbey (1988). The study area has been tectonically stable since the Proterozoic (600–2500 My go). The major landscape features are controlled by the Archaean (2500–3700 My old) granites that underlie most of the study area, and have weathered into gently undulating plains and broad valleys covered by Tertiary soils (< 65 My old). The narrow Forrestania greenstone (Archaean mafic and ultramafic lithologies) belt has several banded ironstone units (formed from lacustrine deposits of iron oxides and quartz sand) up to 30 m thick which form the abrupt ridges of North, Middle and South Ironcap. Some areas of Tertiary laterite were also found associated with the greenstone belt (Chin *et al.* 1984). Gold was first discovered in the Forrestania area in 1915 and there has been a long history of mineral exploration and mining along this belt. There are presently three large mines operating in the area; at Forrestania, Middle Ironcap, and Digger Rocks.

The climate of the region is warm dry mediterranean with warm winters and hot summers. Mean annual rainfall at Hyden is 336 mm, with moderate seasonal variation. The driest year on record was 1972 with 159 mm, and the wettest was 1942 with 572 mm. Most rain falls in winter, generally associated with frontal activity from May through August. Summer rainfall (to 50 mm) is highly erratic and results from thunderstorms. The

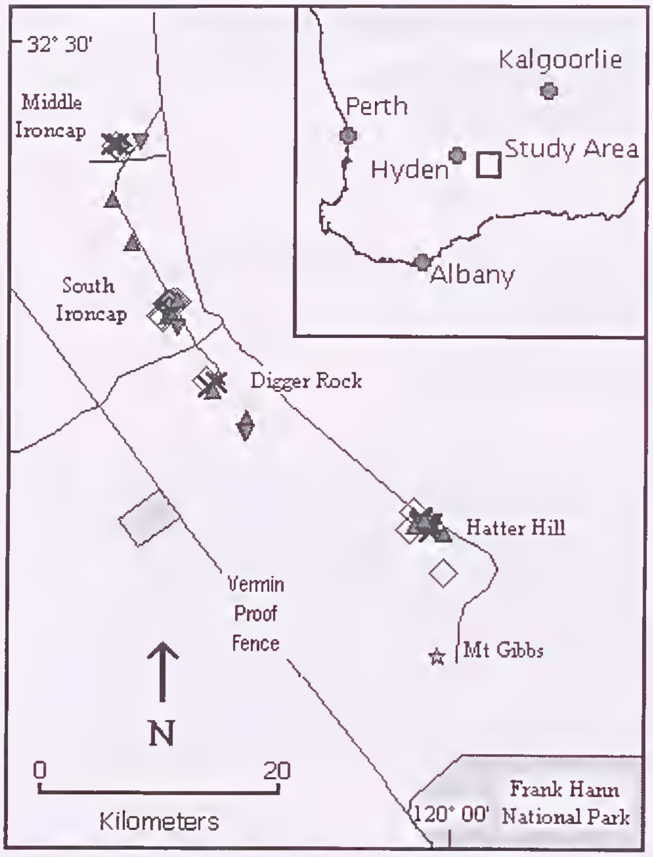

Figure 1. Location of the study area and the distribution of the four communities describes from the southern Forrestania greenstone belt (Middle Ironcap to Hatter Hill). Type 1, open diamond; type 2, solid cross; type 3, solid triangle; type 4 solid inverted triangle.

heaviest rainfalls (to 160 mm) are associated with rain-bearing depressions forming from tropical depressions (Newbey 1988, Anon 1988). The temperature data from Hyden show mean maximum temperature is highest in January (33.4 °C) with December through April all recording mean annual temperatures above 30 °C. Lowest mean minimum temperatures of below 5 °C are recorded in July and August.

The Forrestania greenstone belt lies within the Roe Botanical District, an area characterized by mallee vegetation with some eucalypt woodland in lower valleys and scrub heath and *Allocasuarina* thicket on the residual plateau soils (Beard 1990). Beard (1972) first described the major structural formations of this area and grouped them into vegetation systems. Beard (1972) defined the vegetation of the greenstone belt stretching from Mt Holland to Hatter Hill as the Forrestania system. This system also included granites, quartzites, and banded ironstones that formed prominent rocky ridges. Beard described sclerophyll woodlands of *Eucalyptus salmonophloia* and *E. longicornis* but noted that these areas had been extensively cut and burnt over and were in poor condition. Very few areas of this vegetation type were encountered during the current survey.

A peculiar feature of the Forrestania system was the ridges of banded ironstone (Beard 1972), with Mt Holland being covered by a dense thicket whose dominants included *Allocasuarina campestris*, *Calothamnus asper*, *Hakea* sp, *Dryandra* sp, and *Callitris preissii* subsp *verrucosa* (syn *C. tuberculata*). Further south at South Ironcap the vegetation was a heath with occasional scattered *E. falcata* (syn *E. rugulata*). Shrubs recorded included *Banksia sphaerocarpa*, *Allocasuarina ?dielsiana*, *Isopogon gardneri*, *Melaleuca ?cardiophylla*, *Grevillea insignis*, *Adenanthos viridiflorus*, *Isopogon teretifolius*, *Callitris roei*, *Calothamnus quadrifidus*, *Lysinema ciliatum*, *Lasiopetalum* sp and *Dryandra viscida*. At Hatter Hill, a further 25 km south-east, the rocky greenstone ridges were covered with thickets of *Allocasuarina ?dielsiana*, and *Eucalyptus loxophleba* with *Cassia chatelainiana*, *Dodonaea stenozyga*, *Melaleuca acuminata*, *Calothamnus quadrifidus*, *Boronia inornata* and *Westringia dampieri*.

Following Beard's work in the area a series of regional surveys were undertaken across the eastern goldfields. In the report covering the Lake Johnson–Hyden area, Newbey & Hnatiuk (1988) detail the regional vegetation patterns following a land system approach. They note that the three Ironcaps (North, Middle and South) vary slightly in their fine grain mosaic of vegetation structure and more so in species composition. They further note that the vegetation and flora of these ironstones differ widely from the nearest other banded ironstone formation. The major vegetation type of the greenstone belt from Mt Holland to Hatter Hill is *Eucalyptus flocktoniae* (syn *E. urna*) low woodland which differs from the Parker Range and Highclere Hills to the north (Newbey & Hnatiuk 1988). Growing in the *E. flocktoniae* low woodlands were other low trees of *E. salubris*, and *E. annulata*, with tall shrubs of *Exocarpos aphyllus*, *Melaleuca cucullata* and *Melaleuca pauperiflora*. Breakaways, a common component of goldfield ranges, were only recorded once but mallees of *Eucalyptus* aff *wandoo* (syn *Eucalyptus livida*) were usually present in small partially laterized areas. Both Beard's survey and the later biological survey of the eastern goldfields were undertaken to provide regional overviews. Consequently the individual ranges were not sampled extensively.

The aim of the present work was to undertake a detailed floristic survey of the Forrestania greenstone belt form Middle Ironcap to Hatter Hill. This involved the compilation of a detailed flora list, and the description of the vegetation patterning of the area based on a series of permanently located quadrats.

Methods

Thirty-eight 20 m x 20 m quadrats were established on the southern half of the Forrestania greenstone belt from Middle Ironcap south to Hatter Hill (Fig 1). These quadrats attempted to cover the major geographical, geomorphological and floristic variation found in the study area. Care was taken to locate quadrats in the least disturbed vegetation available in the area being sampled.

Within each quadrat all vascular plants were recorded. Quadrats were sampled in early September 1996. Data on topographical position, slope, aspect, percentage litter, percentage bare ground, percentage surface rock (bedrock and surfical deposits), and vegetation structure were collected from each quadrat. Topographical position was scored on a subjective six point scale (ridge tops = 1, upper slopes = 2, midslopes = 3, lower slopes = 4, valley flats =5, small rise in valley =6). Slope was scored on a one to three scale from flat to medium, to steep. Aspect was recorded as one of 16 cardinal directions. Altitude was taken from 1:100000 series topographical map to nearest 10 m. Vegetation structure was recorded using Muir's (1977) classification. All quadrats were permanently marked with four steel fence droppers and their positions fixed using a GPS unit.

Quadrats were classified according to similarities in species composition. In these analyses only perennial species were used to facilitate comparisons with classifications from other ranges (Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2001a,b). The quadrat and species classifications undertaken used the Czekanowski similarity coefficient and "unweighted pair-group mean average" fusion method (UPGMA module in PATN, Belbin 1995, beta value -0.1, Sneath & Sokal, 1973). Semi-strong hybrid (SSH in PATN) ordination of the quadrat data was undertaken to show spatial relationships between quadrat groups (here referred to as community types) and to elucidate possible environmental correlates with the classification (Belbin 1991). Methods of Dufrene & Legendre (1997) were used to determine best indicator taxa for each group (from PC-ORD v 4.24, McCune & Mefford 1999).

Climate estimates (mean annual temperature, annual temperature range, mean annual rainfall, rainfall coefficient of variation) were obtained from BIOCLIM (Busby 1986), a prediction system that uses mathematical surfaces fitted to long term climate data. Relationships among and between physical site parameters and climate estimates was examined using Spearman rank correlation coefficient. To reduce the probability of type I errors given the number of intercorrelations, significance differences were reported at a level of $P<0.01$. Vectors for the physical site parameters, latitude, altitude and climatic estimates were fitted to the ordination along axes of highest correlation using the principal axis correlation routine in the PATN package (Belbin 1995) (also known as rotational correlation analysis). Statistical significance of these vectors was determined using random permutations of the values of the variable among sites (Faith & Norris 1989). Statistical relationships between quadrat groups for physical site parameters and climate estimates were tested using Kruskal-Wallis non-parametric analysis of variance (Siegel 1956).

Nomenclature generally follows Paczkowska and Chapman (2000). Voucher specimens have been be lodged in the Western Australian Herbarium. Introduced taxa are indicated by a "*".

Results

Flora

A total of 343 taxa (species, subspecies, varieties) and two hybrids were recorded from the Forrestania greenstone belt. The flora list was compiled from taxa found in the 38 quadrats or the adjacent area and from collections of the Western Australian Herbarium (Appendix 1). Of these 345 taxa, 342 are native and 3 are weeds. The best represented families were the Myrtaceae (77 taxa), Proteaceae (38 taxa), Mimosaceae (25 taxa), Papilionaceae and Orchidaceae (20 taxa), Asteraceae (17 native taxa and 1 introduced taxon) and Epacridaceae (14 taxa) (Appendix 1). This pattern is typical of the flora of the South Western Botanical Province (Beard 1990). The most common genera were *Eucalyptus* (38 taxa), *Acacia* (25 taxa) and *Melaleuca* (22 taxa).

Thirty-five taxa of conservation significance were recorded from the range. This included;

- three taxa listed as threatened;
- a further 29 that are being considered for listing as threatened flora (Atkins 2001);
- 10 taxa considered endemic to the range; and
- a further eight that are regional endemics (found within 100 km) (Table 1).

One taxon (*Stenanthemum liberum*) was collected for the first time and is only known from two populations (Rye 2001).

During the current survey, new populations of *Boronia revoluta* and *Banksia sphaerocarpa* var. *dolichostyla* (both listed as threatened) were located. This was somewhat surprising given the proximity to active mines and the botanical survey work undertaken associated with their commissioning. A significant range extensions was recorded for *Bentleya diminuta*. This is a very unusual tufted perennial herb (Pittosporaceae) which has small clusters of prostrate leaves connected by thick underground rhizomes. It has previously been recorded from the Cape Arid–Ravensthorpe area.

Vegetation

In the 38 quadrats established south of Middle Ironcap, 229 taxa were recorded of which 202 were perennial. Fifty-seven perennials occurred at only one quadrat. Preliminary analyses showed these singletons had no effect on the community classification and therefore are not discussed further. As a result the final data set consisted of 145 perennial taxa in 38 quadrats. Species richness ranged from seven to 36 taxa per quadrat, with individual taxa occurring in between two and 28 of the 38 quadrats. Only material that could be identified down to species or subspecies level was included in the analysis (ca 95% of records).

The first major division in the dendrogram separates the quadrats on skeletal soils derived from banded ironstone and the massive laterites (community types 1 & 2) from quadrats on deeper soils derived from greenstone or decomposing laterites (community types 3 & 4; Fig 2, Appendix 2).

- Community type 1 is comprised of the species-rich shrublands or mallee shrublands. Species in species groups I and K characterize community type 1 and contain most indicator species (Appendix 2). Average species richness was 27.2 taxa plot^{-1}. This community type was restricted to the massive outcrops along the range (Middle Ironcap, South Ironcap, Digger Rock and Hatter Hill, Fig 1). Three subtypes can be recognized (Appendix 2). Type 1a occurred on all outcrops and was strongly represented by species group I and a lack of species group J which characterized

Table 1

Taxa of conservation significance from the southern Forrestania greenstone belt (Middle Ironcap to Hatter Hill). Three taxa are listed as Declared Rare Flora under Wildlife Conservation Act; 29 are being considered for listing. Ten taxa are considered to be endemic to the range and a further eight which occur on similar landforms within 100 km, are considered to be regional endemics.

Family	Taxon	Conservation status	Endemic status
Dilleniaceae	*Hibbertia axillibarba*	potentially threatened	local
	Hibbertia carinata	potentially threatened	
	Hibbertia lepidocalyx subsp *lepidocalyx*		regional
Droseraceae	*Drosera browniana*		local
Epacridaceae	*Acrotriche patula*	potentially threatened	
	Leucopogon marginatus	threatened	
	Leucopogon sp Ironcaps (N Gibson & K Brown 3070)	potentially threatened	
	Leucopogon sulcatus	potentially threatened	
	Monotoca leucantha	potentially threatened	
Loganiaceae	*Logania exilis*	potentially threatened	regional
Mimosaceae	*Acacia heterochroa* subsp *robertii*	potentially threatened	regional
	Acacia singula	potentially threatened	
	Acacia tetraneura	potentially threatened	
Myoporaceae	*Calamphoreus inflatus*	potentially threatened	
	Eremophila racemosa	potentially threatened	
Myrtaceae	*Eucalyptus exigua*	potentially threatened	
	Eucalyptus georgei subsp *fulgida*	potentially threatened	regional
	Eucalyptus rugulata		local
	Euryomyrtus leptospermoides	potentially threatened	
	Melaleuca agathosmoides	potentially threatened	local
Papilionaceae	*Eutaxia* sp Hatter Hill (KR Newbey 6532)	potentially threatened	regional
	Mirbelia densiflora	potentially threatened	
Pittosporaceae	*Bentleya diminuta*	potentially threatened	
Proteaceae	*Banksia sphaerocarpa* var *dolichostyla*	threatened	regional
	Dryandra ferruginea subsp *flavescens*	potentially threatened	
	Dryandra viscida	potentially threatened	local
	Grevillea insignis subsp *elliotii*	potentially threatened	local
	Grevillea lullfitzii	potentially threatened	local
Rhamnaceae	*Cryptandra intonsa*	potentially threatened	local
	Stenanthemum liberum	potentially threatened	local
Rutaceae	*Boronia revoluta*	threatened	local
	Microcybe pauciflora subsp *grandis*	potentially threatened	regional
	Phebalium brachycalyx	potentially threatened	
Sterculiaceae	*Lasiopetalum* sp Ironcaps (PG Wilson 7024)	potentially threatened	regional
Stylidiaceae	*Stylidium sejunctum*	potentially threatened	

the two quadrats of type 1b. Species group J contained three local and one regional endemic taxa. Type 1b was restricted to area around South Ironcap. Type 1c generally lacked taxa in species groups I and J and was found at Middle Ironcap and Hatter Hill area. Type 1c had slightly lower species richness (mean 23.6) compared with types 1a and 1b (29.1–29.5).

- Community type 2 were generally mallee shrublands or *Allocasuarina* thickets primarily found on massive laterites. Species composition varied from community type 1 by stronger representation from species groups A–D and lower representation from species groups I, J and most taxa in species group K. Indicator species for this community type occurred in species groups B and D (Appendix 2). Species richness tended to be lower than in community type 1 (20.3 taxa plot^{-1}). Distribution of this community was again closely correlated with the massive outcrops at Middle Ironcap, Digger Rock and Hatter Hill, it was not recorded from South Ironcap (Fig 1).
- Community type 3 were eucalypt woodlands dominated or co-dominated by *Eucalyptus urna* and *E. salubris* occurring on the colluvial deposits on the flats below the outcrops or on the broad flat ridges along the range generally with an understorey dominated by *Melaleuca* spp (Fig 1). Species richness was considerably lower (14.4 taxa plot^{-1}) and this community was characterized by species group E –H, with indicator species being concentrated in species group E (Appendix 2). Only one local endemic (*Melaleuca agathosmoides*) is found in these species groups, all the other local and regional endemics are restricted to community types 1 and 2.
- Community type 4 was a species poor mallee community generally dominated by *Eucalyptus calycogona* with large emergent *Eucalyptus salmonophloia* on small colluvial flats in the ranges (Fig 1). One quadrat in this group was dominated by *E. longicornis*. Species richness was low with an average 12.5 taxa plot^{-1}. Indicator species for this community type were *Eucalyptus calycogona*, *Eucalyptus salmonophloia*, and *Olearia muelleri* (Appendix 2).

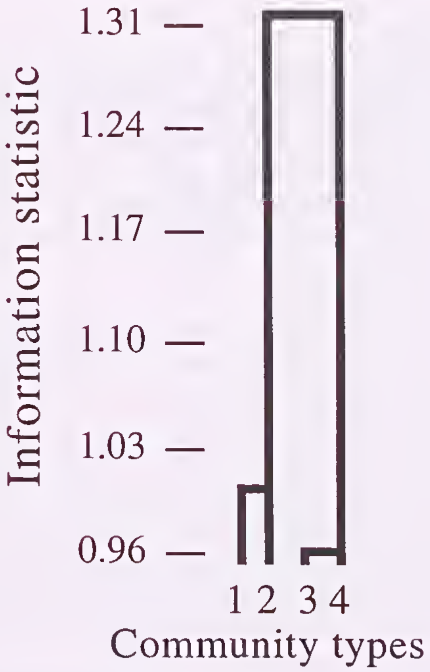

Figure 2. Dendrogram of 4 group level classification of 38 quadrats established along the southern Forrestania greenstone belt between Middle Ironcap and Hatter Hill.

Physical Correlates

The climatic estimates and latitude and altitude showed significant intercorrelations, as did slope class and aspect (Table 2). Topographic position, slope, percent surface rock and percent litter showed significance differences between the mean values of the four community types (Table 3). No significance differences were found for latitude, altitude or the climatic estimates.

Steeper slopes differentiated community types 1 and 2, from 3 and 4, as did a higher percentage of surface rock and rock type (Table 3 & Fig 3). Surfical deposits of banded ironstone and laterite (often massive) occurred at most quadrats in community types 1 and 2 but uncommon in the other community types. Altitude and topographic position scores are somewhat misleading because topographical relief along the range was subdued except near Middle and South Ironcap. The broad intervening ridges where community type 3 was common had a similar topographic position score and altitude as community types 1 and 2 that were restricted to the more pronounced hill and ridge tops. The soil profiles on these broad ridges was much deeper than on the outcrops.

The three dimensional ordination (stress = 0.17) of the 38 quadrats showed clear separation between communities (1 and 2) found on the outcrops and the eucalypt woodlands of the broad ridges and colluvial deposits. The shrublands and mallee shrublands of community type 1 occur in the lower left quadrant, the mallee shrublands and thickets of community type 2 occur in the centre and the woodlands of community type 3 and 4 in the upper right quadrant with segregation between these units (Fig 4). Good separation of the subtypes of community type 1 was found on the third axis (not shown). Of the site parameters only percentage surface rock was significantly correlated with the ordination, correlations could not be improved by standard data transformations, implying no simple non-linear response in the data.

Discussion

The southern Forrestania belt has a similar floral richness to the other goldfields ranges for which detailed information exists but is much richer in local endemics (Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2001a,b; Gibson unpublished data; Table 4). The reasons for this high level of local endemism is not clear; topographically and geologically the range between Middle Ironcap and Hatter Hill is no more diverse than other goldfields ranges nor is the current climatic gradients unusual. The range does form part of the western most greenstone belt, but so to do the Highclere Hills which have no local endemic taxa (Table 4).

The significance of the flora of this area has long been recognized and it is one of the best collected ranges in the goldfields, yet the flora of the range is still poorly known as indicated by the number of taxa requiring further survey to an assessment of their threat status (Table 1) and that the current survey (that was restricted to the existing track network) located new populations of

Table 2

Matrix of Spearman rank correlation coefficients between site physical parameters and climate estimates. Correlation significant at P < 0.01 shown in bold. See methods for parameter codes.

	Position	Slope	Aspect	% rock	% litter	% bare	Latitude	Altitude	Tann	Trange	Rann	Rcv
Position	1.00											
Slope	0.25	1.00										
Aspect	0.22	**0.74**	1.00									
% rock	0.06	0.41	0.17	1.00								
% litter	-0.14	-0.11	-0.03	-0.40	1.00							
% bare	0.04	0.01	0.13	-0.09	-0.12	1.00						
Latitude	0.18	0.15	0.00	0.28	-0.19	0.24	1.00					
Altitude	-0.08	0.04	-0.28	0.36	-0.03	0.09	**0.68**	1.00				
Tann	0.32	0.11	0.39	-0.17	0.05	0.34	**0.44**	-0.26	1.00			
Trange	0.15	0.14	-0.02	0.35	-0.13	0.25	**0.96**	**0.75**	0.36	1.00		
Rann	0.17	-0.01	0.35	-0.30	-0.01	-0.03	**-0.43**	**-0.93**	**0.50**	**-0.51**	1.00	
Rcv	0.30	0.17	0.13	0.21	-0.13	0.26	**0.89**	**0.42**	**0.69**	**0.86**	-0.11	1.00

Table 3

Plant community mean values for topographic position (1 – ridge top to 6 – rises in valley), slope (1 – flat to 3 – steep), aspect (16 cardinal directions), percent exposed rock, percent litter, percent bare ground, latitude, altitude (m), mean annual temperature (°C), annual temperature range (°C), mean annual rainfall (mm), rainfall coefficient of variation (%). Differences between means tested using Kruskal – Wallis non parametric analysis of variance (ns indicates not significant, * indicates $P<0.05$, ** indicates $P < 0.01$)

	Type 1	Type 2	Type 3	Type 4
Physical site parameters				
Position*	2.9	2.1	2.3	5.5
Slope*	2.1	2.0	1.5	1.5
Aspect^{ns}	3.9	4.1	2.4	2.0
% rock**	63.2	57.8	19.1	28.8
% litter*	38.6	47.8	68.2	46.3
% bare^{ns}	22.9	12.2	13.6	26.3
Latitude^{ns}	32.7132	32.7506	32.7370	32.6996
Altitude^{ns}	431.4	413.3	414.5	405.0
Climate estimates				
Tann^{ns}	16.2	16.2	16.2	16.3
Trange^{ns}	27.1	27.0	27.0	27.1
Rann^{ns}	284.2	287.2	287.5	290.5
Rcv^{ns}	40.7	39.8	40.4	41.2
Species richness	27.2	20.3	14.4	12.5
No quadrats	14	9	11	4

threatened flora and a previously uncollected species (Rye 2001).

In biogeographical terms the range was most similar to the Bremer and Parker Ranges with high diversity of eucalypts, acacias and melaleucas, and low richness of *Eremophila* spp. compared to the more northern ranges (Table 4). Another unusual feature of the Forrestania belt is the high richness (9 taxa) of *Hibbertia* spp, a number of which have been recently been named from the range (Wheeler 2000).

Newbey & Hnatiuk (1988) suggested that the three Ironcaps (North, Middle and South) vary in species composition, and while the recent burn precluded sampling of North Ironcap during the present survey the results only partially support this finding. The community types of the banded ironstone and laterite outcrops (types 1 and 2) were not found to be restricted to particular outcrops but were widespread between Middle Ironcap and Hatter Hill (Fig 1), however community type 2 was not recorded from South Ironcap and the two quadrats comprising subtype 1b were restricted to this outcrop.

The current survey does support Newbey & Hnatiuk's (1988) observation that the vegetation and flora of these ironstones differ widely from the nearest other banded ironstone formation, indeed one of the subtypes of community 1 is characterized by a number of locally endemic species (Appendix 2) and nine of the ten local

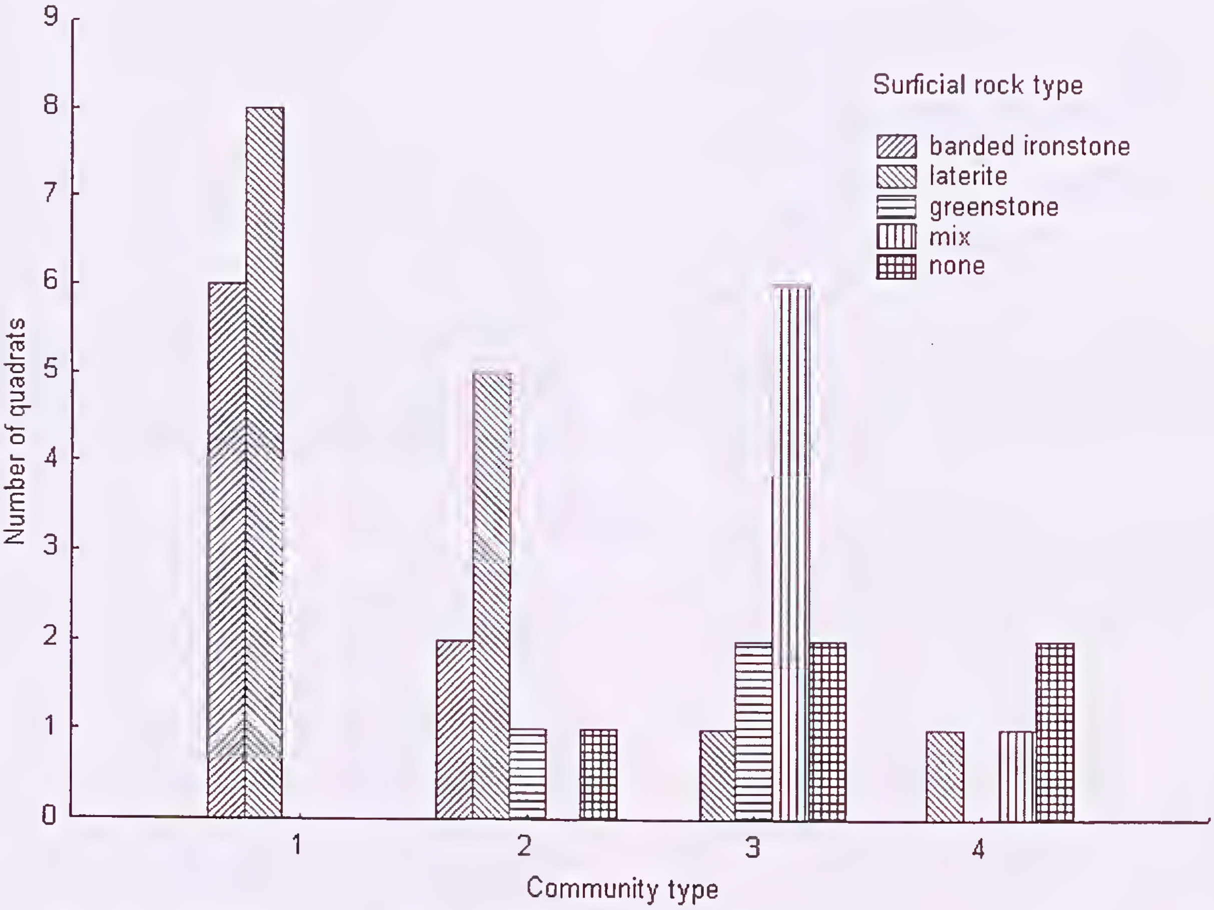

Figure 3. Type of rock seen at the surface in each of the quadrats arranged into the four community types derived from the classification of the perennial plants. The rock material could either be loose or massive, the mix category were loose material to 5 cm diameter and included in all three of the main rock types of the area.

Table 4

Comparison of the floras of the southern Forrestania greenstone belt (Middle Ironcap to Hatter Hill), the Parker Range, the Bremer Range, the Highclere Hills, the Jaurdi uplands, the Helena and Aurora Range, and the Mt Manning Range. Note data from Bremer and Parker Ranges were collect in a dry year and underestimate the annual floras (data from Gibson *et al.* 1997; Gibson & Lyons 1998a,b; Gibson & Lyons 2001a,b; Gibson unpublished data).

	Southern Forrestania belt	Parker Range	Bremer Range	Highclere Hills	Jaudi uplands	Helena & Aurora Range	Mt Manning Range
Flora	345	254	267	242	288	324	238
Weeds	3	10	8	25	15	21	4
Local endemic taxa	10	5	3	–	–	4	–
Taxa – first collections	1	2	2	–	–	1	–
Eucalyptus spp	38	29	30	12	20	19	17
Acacia spp	25	20	17	9	15	17	10
Melaleuca spp	22	14	19	2	4	5	5
Eremophila spp	5	7	11	8	16	14	11

endemics are in fact restricted to the banded ironstone and laterite outcrops of the range.

Mining and exploration has been and continues to be extremely active in the study area and rehabilitation has generally been poor. There is an urgent need for the adoption of high standard environmental management of both exploration and mining operations. Almost none of the Forrestania greenstone belt is currently in the conservation reserve system. Work outlined here and previously reported by Beard (1972) and Newbey & Hnatiuk (1988) indicate a number of plant communities and at least 10 species are restricted to this area. The small Lake Cronin Nature Reserve (1016 ha) which lies between Middle Ironcap and Mt Holland is the only reserve covering the Forrestania vegetation system. None of the banded ironstone or associated lateritic areas are currently reserved. There is an urgent need for a series of nature reserves along the Forrestania belt.

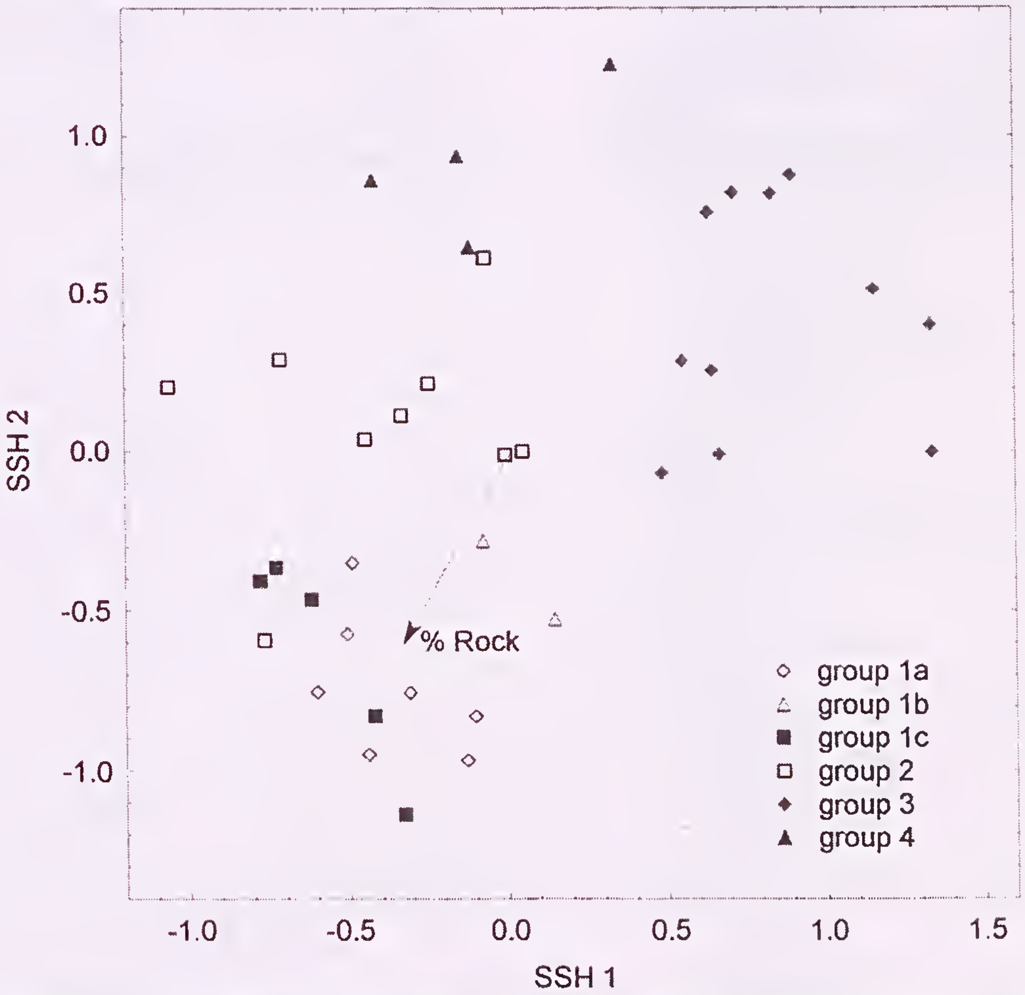

Figure 4. Ordination of the 38 quadrats coded by community type. Arrow shows the direction of the best fit linear correlation with percent surface rock. No other site parameter showed a significant correlation with the ordination.

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Appendix 1

Flora list for southern Forrestania greenstone belt between Middle Ironcap and Hatter Hill, includes all taxa from the sampling quadrats and adjacent areas and collections lodged in the Western Australian Herbarium. Nomenclature generally follows Paczkowska and Chapman (2000), * indicates an introduced taxon.

- Amaranthaceae
  - *Ptilotus holosericeus*
- Anthericaceae
  - *Thysanotus patersonii*
- Apiaceae
  - *Daucus glochidiatus*
  - *Hydrocotyle rugulosa*
  - *Platysace maxwellii*
  - *Trachymene ornata*
- Apocynaceae
  - *Alyxia buxifolia*
- Asteraceae
  - *Angianthus tomentosus*
  - *Asteridea athrixioides*
  - *Blennospora drummondii*
  - *Brachyscome perpusilla*
  - *Hyalosperma demissum*
  - * *Hypochaeris glabra*
  - *Isoetopsis graminifolia*
  - *Millotia tenuifolia*
  - *Olearia dampieri* subsp *eremicola*
  - *Olearia muelleri*
  - *Olearia ramosissima*
  - *Podolepis lessonii*
  - *Podolepis tepperi*
  - *Rhodanthe laevis*
  - *Rhodanthe pygmaea*
  - *Senecio glossanthus*
  - *Senecio hispidulus*
  - *Senecio quadridentatus*
- Boraginaceae
  - *Halgania andromedifolia*
  - *Halgania integerrima*
  - *Halgania lavandulacea*
- Boryaceae
  - *Borya sphaerocephala*
- Brassicaceae
  - *Lepidium rotundum*
- Caesalpiniaceae
  - *Labichea stellata*
- Casuarinaceae
  - *Allocasuarina acutivalvis*
  - *Allocasuarina campestris*
  - *Allocasuarina thuyoides*
- Celastraceae
  - *Psammomoya choretroides*
- Centrolepidaceae
  - *Centrolepis cephaloformis* subsp *cephaloformis*
- Chenopodiaceae
  - *Chenopodium* sp
  - *Sclerolaena diacantha*
- Convolvulaceae
  - *Wilsonia humilis*
- Crassulaceae
  - *Crassula colorata*
- Cupressaceae
  - *Callitris canescens*
  - *Callitris roei*
  - *Callitris tuberculata*
- Cyperaceae
  - *Lepidosperma* aff *brunonianum* (NG & KB 2509)
  - *Lepidosperma* sp (NG & KB 2512)
  - *Lepidosperma* sp (NG & KB 3739)
  - *Schoenus nanus*
- Dasypogonaceae
  - *Lomandra* sp
- Dilleniaceae
  - *Hibbertia* aff *pungens* (NG & KB 2523)
  - *Hibbertia axillibarba*
  - *Hibbertia carinata*
  - *Hibbertia exasperata*
  - *Hibbertia gracilipes*
  - *Hibbertia hemignosta*
  - *Hibbertia lepidocalyx* subsp *lepidocalyx*
  - *Hibbertia pungens*
  - *Hibbertia rostellata*
- Droseraceae
  - *Drosera browniana*
  - *Drosera glanduligera*
  - *Drosera lowriei*
  - *Drosera macrantha*
- Epacridaceae
  - *Acrotriche patula*
  - *Astroloma serratifolium*
  - *Coleanthera myrtoides*
  - *Leucopogon conostephioides*
  - *Leucopogon cuneifolius*
  - *Leucopogon dielsianus*
  - *Leucopogon fimbriatus*
  - *Leucopogon marginatus*
  - *Leucopogon* sp Ironcaps (NG & KB 3070)
  - *Leucopogon* sp Wheatbelt (S Murray 257)
  - *Leucopogon sulcatus*
  - *Lysinema ciliatum*
  - *Monotoca leucantha*
  - *Styphelia pulchella*
- Euphorbiaceae
  - *Beyeria brevifolia*
- Geraniaceae
  - *Pelargonium havlasae*
- Goodeniaceae
  - *Coopernookia strophiolata*
  - *Dampiera angulata*
  - *Dampiera haematotricha* subsp *dura*
  - *Goodenia helmsii*
  - *Goodenia laevis* subsp *humifusa*
  - *Goodenia pinifolia*
  - *Scaevola spinescens*
- Haemodoraceae
  - *Conostylis argentea*
- Haloragaceae
  - *Glischrocaryon aureum* var *angustifolium*
  - *Haloragodendron glandulosum*
- Juncaceae
  - *Juncus flavidus*
- Juncaginaceae
  - *Triglochin calcitrapa*
- Lamiaceae
  - *Cyanostegia lanceolata*
  - *Hemigenia* sp Newdegate (E Bishop 75)
  - *Hemigenia teretiuscula*
  - *Hemigenia westringioides*
  - *Microcorys obovata*
  - *Westringia cephalantha*
  - *Westringia rigida*
- Lauraceae
  - *Cassytha aurea*
  - *Cassytha glabella*
  - *Cassytha melantha*
  - *Cassytha racemosa*
- Lobeliaceae
  - *Isotoma scapigera*

- Loganiaceae
  - *Logania exilis*
  - *Logania flaviflora*
  - *Logania judithiana*
  - *Logania perryana*
- Mimosaceae
  - *Acacia andrewsii*
  - *Acacia binata*
  - *Acacia brachyclada*
  - *Acacia brachyphylla* var *brachyphylla*
  - *Acacia castanostegia*
  - *Acacia deficiens*
  - *Acacia erinacea*
  - *Acacia evenulosa*
  - *Acacia hemiteles*
  - *Acacia heterochroa* subsp *robertii*
  - *Acacia merrallii* x *poliochroa*
  - *Acacia intricata*
  - *Acacia lasiocalyx*
  - *Acacia merrallii*
  - *Acacia moirii* subsp *recurvistipula*
  - *Acacia poliochroa*
  - *Acacia prainii*
  - *Acacia quinquenervia*
  - *Acacia singula*
  - *Acacia* sp Lake King (R Hnatiuk 760791)
  - *Acacia sulcata* var *platyphylla*
  - *Acacia tetraneura*
  - *Acacia uncinella*
  - *Acacia unifissilis*
  - *Acacia yorkrakinensis*
- Myoporaceae
  - *Calamphoreus inflatus*
  - *Eremophila decipiens* subsp *decipiens*
  - *Eremophila densifolia* subsp *pubiflora*
  - *Eremophila psilocalyx*
  - *Eremophila racemosa*
  - *Eremophila saligna*
- Myrtaceae
  - *Aluta appressa*
  - *Astartea ambigua*
  - *Baeckea* sp Merredin (KR Newbey 2506)
  - *Beaufortia micrantha*
  - *Beaufortia schaueri*
  - *Calothamnus quadrifidus*
  - *Calytrix breviseta* subsp *stipulosa*
  - *Chamelaucium ciliatum*
  - *Eremaea* sp
  - *Eucalyptus* aff *calycogona*
  - *Eucalyptus alipes*
  - *Eucalyptus annulata*
  - *Eucalyptus calycogona* subsp *calycogona*
  - *Eucalyptus capillosa* subsp *polyclada*
  - *Eucalyptus celastroides* subsp *virella*
  - *Eucalyptus conglobata*
  - *Eucalyptus cylindriflora*
  - *Eucalyptus cylindrocarpa*
  - *Eucalyptus dendrosheath* ms
  - *Eucalyptus densa* subsp *densa*
  - *Eucalyptus eremophila*
  - *Eucalyptus exigua*
  - *Eucalyptus georgei* subsp *fulgida*
  - *Eucalyptus gratiae*
  - *Eucalyptus grossa*
  - *Eucalyptus kondininensis* subsp *kondininensis*
  - *Eucalyptus livida*
  - *Eucalyptus longicornis*
  - *Eucalyptus loxophleba* subsp *lissophloia*
  - *Eucalyptus myriadena* subsp *myriadena*
  - *Eucalyptus olivina*
  - *Eucalyptus phaenophylla* subsp *interjacens*
  - *Eucalyptus phaenophylla* subsp *phaenophylla*
  - *Eucalyptus phenax*
  - *Eucalyptus pileata*
  - *Eucalyptus prolensa*
  - *Eucalyptus quadrans*
  - *Eucalyptus rigidula*
  - *Eucalyptus rugulata*
  - *Eucalyptus salmonophloia*
  - *Eucalyptus salubris*
  - *Eucalyptus sporadica*
  - *Eucalyptus subtenuis*
  - *Eucalyptus tenera*
  - *Eucalyptus transcontinentalis*
  - *Eucalyptus urna*
  - *Eucalyptus yilgarnensis*
  - *Euryomyrtus leptospermoides*
  - *Leptospermum fastigiatum*
  - *Leptospermum nitens*
  - *Leptospermum spinescens*
  - *Melaleuca acuminata* subsp *acuminata*
  - *Melaleuca adnata*
  - *Melaleuca agathosmoides*
  - *Melaleuca cliffortioides*
  - *Melaleuca cordata*
  - *Melaleuca coronicarpa*
  - *Melaleuca cucullata*
  - *Melaleuca halmaturorum*
  - *Melaleuca johnsonii*
  - *Melaleuca lanceolata*
  - *Melaleuca lateriflora* subsp *lateriflora*
  - *Melaleuca laxiflora*
  - *Melaleuca pauperiflora* subsp *pauperiflora*
  - *Melaleuca pentagona*
  - *Melaleuca phoidophylla*
  - *Melaleuca pungens*
  - *Melaleuca quadrifaria*
  - *Melaleuca rigidifolia*
  - *Melaleuca sapientes*
  - *Melaleuca* sp Hatters Hill (NG & KB 2516)
  - *Melaleuca teuthidoides*
  - *Melaleuca uncinata*
  - *Micromyrtus erichsenii*
  - *Micromyrtus racemosa*
  - *Micromyrtus triptycha* subsp *elata*
  - *Thryptomene kochii*
  - *Verticordia chrysantha*
- Orchidaceae
  - *Caladenia doutchiae*
  - *Caladenia microchila*
  - *Caladenia pachychila*
  - *Caladenia paradoxa*
  - *Caladenia saccharata*
  - *Caladenia sigmoidea*
  - *Cyanicula amplexans*
  - *Diuris laxiflora*
  - *Diuris porrifolia*
  - *Eriochilus dilatatus*
  - *Genoplesium nigricans*
  - *Microtis media* subsp *media*
  - *Oligochaetochilus muticus*
  - *Oligochaetochilus sanguineus*
  - *Oligochaetochilus sargentii*
  - *Pterostylis* aff *aspera*
  - *Pterostylis* aff *barbata*
  - *Pterostylis recurva*
  - *Pterostylis* sp (S Barrett 553)
  - *Thelymitra* aff *macrophyllum*
- Papilionaceae
  - *Bossiaea preissii*
  - *Daviesia benthamii* subsp *acanthoclona*
  - *Daviesia euryloba*
  - *Daviesia nematophylla*
  - *Dillwynia uncinata*

- *Eutaxia parvifolia*
- *Eutaxia* sp Hatter Hill (KR Newbey 6532)
- *Gastrolobium floribundum*
- *Gastrolobium melanocarpum*
- *Gastrolobium nutans*
- *Gastrolobium spinosum*
- *Glycyrrhiza acanthocarpa*
- *Gompholobium gompholobioides*
- *Gompholobium viscidulum*
- *Mirbelia densiflora*
- *Mirbelia dilatata*
- *Pultenaea arida*
- *Pultenaea vestita*
- *Templetonia battii*
- *Templetonia sulcata*

- Pittosporaceae
  - *Bentleya diminuta*
- Pittosporaceae
  - *Billardiera coriacea*
- Plantaginaceae
  - *Plantago* aff *hispidula* (NG & KB 3179)
- Poaceae
  - *Austrodanthonia caespitosa*
  - *Austrostipa acrociliata*
  - *Austrostipa elegantissima*
  - *Austrostipa platychaeta*
  - * *Bromus rubens*
  - *Neurachne alopecuroidea*
  - *Triodia rigidissima*
- Polygalaceae
  - *Comesperma volubile*
- Portulacaceae
  - *Calandrinia* sp (NG & KB 3728)
- Primulaceae
  - * *Anagallis arvensis*
- Proteaceae
  - *Adenanthos argyreus*
  - *Banksia audax*
  - *Banksia elderiana*
  - *Banksia laevigata* subsp *fuscolutea*
  - *Banksia sphaerocarpa* var *dolichostyla*
  - *Banksia violacea*
  - *Conospermum brownii*
  - *Dryandra erythrocephala* var *erythrocephala*
  - *Dryandra ferruginea* subsp *flavescens*
  - *Dryandra pallida*
  - *Dryandra purdieana*
  - *Dryandra viscida*
  - *Grevillea acuaria*
  - *Grevillea anethifolia*
  - *Grevillea cagiana*
  - *Grevillea decipiens*
  - *Grevillea huegelii*
  - *Grevillea insignis* subsp *elliotii*
  - *Grevillea lullfitzii*
  - *Grevillea nematophylla*
  - *Grevillea pilosa* subsp *pilosa*
  - *Hakea commutata*
  - *Hakea erecta*
  - *Hakea meisneriana*
  - *Hakea multilineata*
  - *Hakea scoparia*
  - *Hakea subsulcata*
  - *Isopogon gardneri*
  - *Isopogon scabriusculus* subsp. *stenophyllus*
  - *Isopogon* sp Newdegate (DB Foreman 771)
  - *Isopogon* sp Watheroo (D Foreman 477)
  - *Persoonia helix*
  - *Persoonia saundersiana*
  - *Persoonia striata*
  - *Petrophile circinata*
  - *Petrophile glauca*
  - *Petrophile stricta*
  - *Synaphea interioris*
- Rhamnaceae
  - *Cryptandra intonsa*
  - *Cryptandra minutifolia* subsp *minutifolia*
  - *Cryptandra myriantha*
  - *Cryptandra spyridioides*
  - *Cryptandra wilsonii*
  - *Spyridium mucronatum* subsp *mucronatum*
  - *Stenanthemum liberum*
  - *Trymalium myrtillus* subsp *myrtillus*
- Rubiaceae
  - *Opercularia hispidula*
- Rutaceae
  - *Boronia inornata* subsp *inornata*
  - *Boronia inornata* subsp *leptophylla*
  - *Boronia revoluta*
  - *Drummondita hassellii*
  - *Eriostemon* sp
  - *Microcybe albiflora*
  - *Microcybe pauciflora* subsp *grandis*
  - *Phebalium ambiguum*
  - *Phebalium brachycalyx*
  - *Phebalium filifolium*
  - *Phebalium tuberculosum* x *canaliculatum*
  - *Phebalium tuberculosum*
- Santalaceae
  - *Exocarpos aphyllus*
  - *Santalum acuminatum*
- Sapindaceae
  - *Dodonaea bursariifolia*
  - *Dodonaea ceratocarpa*
  - *Dodonaea glandulosa*
  - *Dodonaea pinifolia*
  - *Dodonaea ptarmicaefolia*
  - *Dodonaea stenozyga*
  - *Dodonaea viscosa* subsp *angustissima*
- Solanaceae
  - *Solanum capsiciforme*
  - *Solanum simile*
  - *Symonanthus aromaticus*
- Stackhousiaceae
  - *Stackhousia monogyna*
- Sterculiaceae
  - *Lasiopetalum* sp Ironcaps (PG Wilson 7024)
- Stylidiaceae
  - *Stylidium breviscapum*
  - *Stylidium sejunctum*
- Thymelaeaceae
  - *Pimelea angustifolia*
- Zygophyllaceae
  - *Zygophyllum glaucum*
  - *Zygophyllum ovatum*

Appendix 2

Sorted two-way table of quadrats established between Middle Ironcap and Hatter Hill showing species occurrence by community type. Quadrats appear as columns and species as rows. Taxa in bold are indicator species identified by INDVAL (Dufrene & Legendre 1997) at four group level ($P < 0.05$), statistical significance tested by randomization procedure.

	Community type					
	1a	1b	1c	2	3	4
SPECIES GROUP A						
Acacia andrewsii				**		
Diuris laxiflora				**		
Stackhousia monogyna				**		
Drosera browniana	*			*		
Olearia dampieri subsp *eremicola*	*			*		
Triodia rigidissima				* *		
SPECIES GROUP B						
Acrotriche patula				****		
Callitris canescens				** *		
Eriochilus dilatatus				** *		
Austrodanthonia caespitosa				**** *		
Thysanotus patersonii	*		*	* ** *	*	*
Cryptandra wilsonii				**		
Westringia rigida		*		**	*	
Diuris porrifolia				**		
Eucalyptus livida	* *			***		
SPECIES GROUP C						
Allocasuarina acutivalvis			*	* *		
Micromyrtus erichsenii				* *		
Banksia laevigata subsp *fuscolutea*			***	*		
Hakea scoparia			* *	* *		
SPECIES GROUP D						
Beyeria brevifolia	*		*	**		
Phebalium brachycalyx	*			*		
Grevillea lullfitzii	* *			*		*
Cryptandra intonsa	*	*		**		
Westringia cephalantha				**		
Caladenia paradoxa			*	*** * *		*
Platysace maxwellii				** * **		
Melaleuca uncinata	*		*	*** **	*	
Dodonaea bursariifolia				*** **		*
Santalum acuminatum	* *		*	* * **		
Eucalyptus phenax				***	* *	*
Olearia muelleri				** **	* *	****
Eucalyptus eremophila				***	**	*
Thelymitra aff *macrophyllum*		*	* **	***** *	**	*
Pterostylis sp (S Barrett 553)		*	*	*	* **	
SPECIES GROUP E						
Acacia erinacea		*		**	**	**
Austrostipa elegantissima				* **	***	**
Grevillea huegelii				*	*	*
Eucalyptus calycogona* subsp *calycogona					* *	***
Eucalyptus salmonophloia					* *	***
Eucalyptus cylindrocarpa	*				*	*
Caladenia microchila				* *	* *	*
Caladenia sigmoidea				*	*	
Grevillea acuaria				* *	*** *	*
Boronia inornata subsp *leptophylla*				*	** *	
Melaleuca teuthidoides					*** *	
Daviesia nematophylla					* ** **	**
Melaleuca adnata				* *	*** *	**
Microtis media* subsp *media			*		*****	
Pultenaea arida					* *****	*
Dodonaea stenozyga					**** ****	*
Eucalyptus annulata					** ***	
Eucalyptus salubris					***** *	
Melaleuca cucullata					* *** ***	
Eucalyptus urna				* * *	******* *	*

				Community type		
	1a	1b	1c	2	3	4
Exocarpos aphyllus	*			* * *	* *** ** *	
__*Melaleuca pauperiflora* subsp *pauperiflora*__					** ****	
__*Microcybe albiflora*__					*** * *	
Eremophila psilocalyx				*	* *	
Oligochaetochilus muticus				** *	* ***	
SPECIES GROUP F						
Melaleuca agathosmoides					* *	
Melaleuca phloidophylla					* *	
__*Melaleuca coronicarpa*__					* * **	
SPECIES GROUP G						
Cryptandra minutifolia subsp _minutifolia_				*	*	
Trymalium myrtillus subsp _myrtillus_					* *	
Hakea commutata					* *	*
Melaleuca cliffortioides					* *	
Melaleuca lateriflora subsp _lateriflora_				*	* *	
Melaleuca pentagono				*	*	
SPECIES GROUP H						
Acacia intricata					* *	*
__*Austrostipa platychaeta*__						**
Ptilotus holosericeus					*	*
__*Eremophila decipiens* subsp *decipiens*__						* *
__*Templetonia sulcata*__						* **
Melaleuca lanceolota					**	*
Sclerolaena diacantha					**	
SPECIES GROUP I						
Acacia brachyphylla var. _brachyphylla_	**					
Leucopogon sp Ironcaps (NG & KB 3070)	* **			*		
Banksia sphaerocarpa var. _dolichostyla_	*	**				
Dampiera anguloia	*	*				
Callitris roei	* *	*				
Lasiopetalum sp Ironcaps (PGW 7024)	* **	*				
__*Lepidosperma* sp (NG & KB 2509)__	****	*				
Calothamnus quadrifidus	* * *	*	*	* *		
Euryomyrtus leptospermoides	*	*	*			
Adenanthos argyreus	***	*				
__*Beaufortia schaueri*__	***	**				
__*Gastrolobium spinosum*__	****	*				
Hibbertia axillibarba	**					
__*Dryandra pallida*__	*****	**	*			
__*Melaleuca pungens*__	******	*	*	* *		
__*Petrophile glauca*__	**	**	*			
Gastrolobium nutans	* *****	*		** *		
Hibbertia aff _pungens_ (NG & KB 2523)	* * *	**		* *		
SPECIES GROUP J						
Acacia castanostegia	* *	*				
Stenanthemum liberum	*	*				
Acacia heterochroa subsp _robertii_		**				
Hibbertia hemignosta		**				
Boronia revoluta	*	**				
Eucalyptus rugulata	*	**				
Oligochaetochilus sanguineus		**		* *	**** *	*
Oligochaetochilus sargentii	*	**	**		*	*
Lepidosperma sp. (NG & KB 2512)		*		*		
Neurachne alopecuroidea		*				*
Pterostylis recurva		*		*		
SPECIES GROUP K						
Acacia singula	** *		*			
__*Hakea multilineata*__	* * *		* *			
Acacia unciuella	*** *		*	*		
__*Goodenia pinifolia*__	*** **	*	*			
__*Persoonia helix*__	*** **					
__*Isopogon gardneri*__	*** *	**	*			

	Community type						
	1a	1b	1c	2	3	4	
Leptaspermum fastigiatum	***		**				
Dryandra viscida	*****	*					
Grevillea insignis subsp *elliotii*	** *						
Eucalyptus olivina	**		*	*			
Leucopagan cuneifolius	* **		*				
Hemigenia teretiuscula	** *				* *		
Acacia sulcata var *platyphylla*		*	*	*			
Dodonaea pinifolia			**	*			
Stylidium sejunctum			***	* *	*		
Hibbertia lepidocalyx subsp *lepidocalyx*	* **		**	* *			
Lepidosperma sp (NG & KB 3739)	* *		****	* *			
Allacasuarina campestris	*******	*	***	** * **	*		
Drasera macrantha	*******	**	****	**** **			
Melaleuca cordata	*******	**	*****	*	*		
Caladenia saccharata	*******	**	****	*********	* **	***	
Astraloma serratifalium	***** *	*	****	** *	*		
Hakea subsulcata	*** ***	**	** *	* *			
Camesperma valubile	* ***		****	***** *			
Calytrix breviseta subsp *stipulosa*	****		* **				
Verticordia chrysantha	* **		***				
Drummandita hassellii	******	*	** *	*			
Stylidium breviscapum	*****		*****	*			
Micramyrtus racemasa	*** *		*****				
Phebalium ambiguum	* ****		* * *	*	*		
Psammamaya charetroides	***		*** *	*			
SPECIES GROUP L							
Allacasuarina thuyoides	* *		** *				
Hibbertia carinata	*		**				
Beaufartia micrantha			** *				
Hibbertia rastellata			* *				
Phebalium filifalium			* *			*	
Isopogon scabriusculus subsp *stenophyllus*	*		* *				
Leucopogon sp Wheatbelt (S.Murray 257)			* *				
Hibbertia gracilipes	*	*	*				
Phebalium tuberculasum	*		* *	* *			
Thryptomene kochii	*		*				

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Vegetation classification and ordination of the central Hamersley Ranges, Western Australia

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Abstract

Vegetation studies of Australian mountainous deserts are limited. The Hamersley Ranges region of north-west Australia is such an environment. It comprises a series of ranges and other uplands which rise above an extensive plateau. Geologically the region is complex (bedrocks range from Archaean granites & gneisses to Proterozoic sedimentary ironstones to Tertiary limestone to various colluvial and alluvial deposits). At 139 sites within the central portion of the Ranges, the cover, frequency and abundance of perennial plant species were measured. The data were used to construct a site dissimilarity matrix using the Bray-Curtis measure. Both hierarchical (flexible-UPGMA) and non-hierarchical (ALOC) classification procedures were used on this matrix to derive a vegetation classification consisting of 16 plant communities, 2 vegetation types and 8 sub-types. Each community is described in detail and contrasted in terms of floristics, life-forms, structure and indicator species. Ordination (using a hybrid form of multidimensional scaling) showed intergradation of communities in terms of species composition, although the lowland communities were found to be relatively distinct from the uplands and pediment slopes. A floristic gradient along the topographic profile from mountain/hill top to valley floor was identified in the ordination space and characterised in terms of dominant species. A differential profile constructed for such floristic gradient found that, spatially, the transition zones between communities varied in width and other characteristics. It is hoped that the classification scheme and the methodology developed here will serve as a foundation for the whole Hamersley Ranges region.

Keywords: vegetation, plant communities, classification, arid climate, Pilbara, Hamersley Ranges

Introduction

Extensive areas of hot desert with mountainous terrain are found on all continents with the exception of Antarctica and Europe (Evenari *et al.* 1985). Plant communities and other vegetation types have been determined and described for a large number of such areas (Goodall & Perry 1981; Evenari *et al.* 1985). Although they have employed a variety of classification approaches, such studies have regularly demonstrated or described the distinctiveness of plant communities, both spatially and in terms of species composition. Such vegetation patterning has often been attributed to the distinctiveness of landforms in such regions (Ayyad 1981; Wierenga *et al.* 1987; Abbas *et al.* 1991; Cowlishaw & Davies 1997). For instance, typical desert landforms, such as hill slopes, pediments, bajadas, playas and regs, are often reported as having characteristic plant communities with relatively sharp boundaries between communities. Other authors have shown that, although some landforms have characteristic communities and dominant species, measurable gradients in species composition occur in the landscape in response to environmental gradients linked to gradually decreasing slopes and/or altitude (Ezcurra *et al.* 1987; Cornelius *et al.* 1991; Ghazanfar 1991; Parker 1991; Vetaas 1992; Patten & Ellis 1995). This often results in broad transition zones between communities (i.e. ecoclines), especially along subdued slopes of the piedmont ("foot of the mountain") zone. Where vegetation studies have been regional rather than local in extent, various geological substrates and climatic gradients are likely to be encountered, which further complicates variation patterns. There are some reports of different communities on the same landform in response to different types of parent rocks (Danin & Orshan 1990; Ward *et al.* 1993), whilst others have reported geological control on vegetation to be secondary to landform (Parker 1991).

Mountainous deserts cover about 12% of Australia's extensive arid zone (Mabutt 1977; Williams & Calaby 1985). They are generally of much lower relief than mountainous deserts elsewhere, but tend to show the same broad pattern of landforms. Examples include the Macdonnell, Flinders, Central and Hamersley Ranges. The Hamersley Ranges cover an extensive area of approximately 60 000 km^2 within the arid, north-west of Australia (Fig 1). The Ranges consist of a series of east-west trending mountain ranges rising above an extensive plateau. Between the ranges are broad drainage systems. Previous vegetation studies of the Ranges are limited and comprise a regional delineation and mapping of "communities" at a broad (1:1 000 000) map scale (Beard 1975) and several local, fine-scale studies of areas subject to mining developments, typically around 100 km^2 in extent (e.g. Trudgen & Casson 1998). Between these two extremes in scale, vegetation descriptions are absent. Furthermore, it is common for vegetation units in such studies to be defined subjectively and on the basis of physiognomy and dominant species, rather than overall floristic differences. This paper aims to fill this void by determining and describing vegetation types and communities in the central portion of the Hamersley Ranges using floristic data and multivariate methods. The degree to which vegetation units are floristically and spatially distinct will also be addressed. It is hoped that the vegetation classification and the methodology established here will form the basis for a classification scheme for the whole Hamersley Ranges region. Such a classification scheme would be of considerable benefit to those involved in conservation planning and impact assessment throughout the region, particularly as the amount of development is expected to increase dramatically over the next decade.

Methods

Study area

The study area was located within the central portion of the Hamersley Ranges some 1100 km north of Perth, and was approximately 120 x 80 km in size (Fig 1). The area is dominated by Karijini National Park and is situated between the towns of Newman, Tom Price and Wittenoom (Fig 1). The Hamersley Ranges are located on the Hamersley Plateau, an extensive area which gently rises from north of the Ashburton River and ends in a sharp escarpment at the Fortescue River floodplain. The plateau surface lies 600–700 m above sea level. A series of east to west trending ranges and associated hills and mountains rise above the plateau a further 200 to 600 m. Characteristic landforms of the region are similar to those of other mountainous deserts (Cooke *et al.* 1993) and include: 1) slopes of hills, ridges and mountains; 2) pediment slopes (slopes of sorted colluvium at the base of hills, ridges, etc.); 3) bajada slopes (coalesced alluvial fans below pediments); 4) alluvial flats and broad drainage lines; 5) confined streams and creeklines; and 6) cuesta (scarp and dip slope topography) (Lorimer 1991). The surface geology of the Ranges is dominated by ironstones on the uplands and, in the broad valley systems, various formations of colluvium and alluvium. Ironstones date from the lower Proterozoic era when layers of iron rich sediment are believed to have been deposited while the area was inundated by sea (Twidale & Campbell 1991). A number of ironstone formations occur in the Ranges and they typically alternate with layers of dolomite and shale. In addition to these sedimentary rocks, Archaean (basement) granites and gneiss are found, predominantly in the south of the study area. Volcanic intrusions (mainly dolerite sills) are also

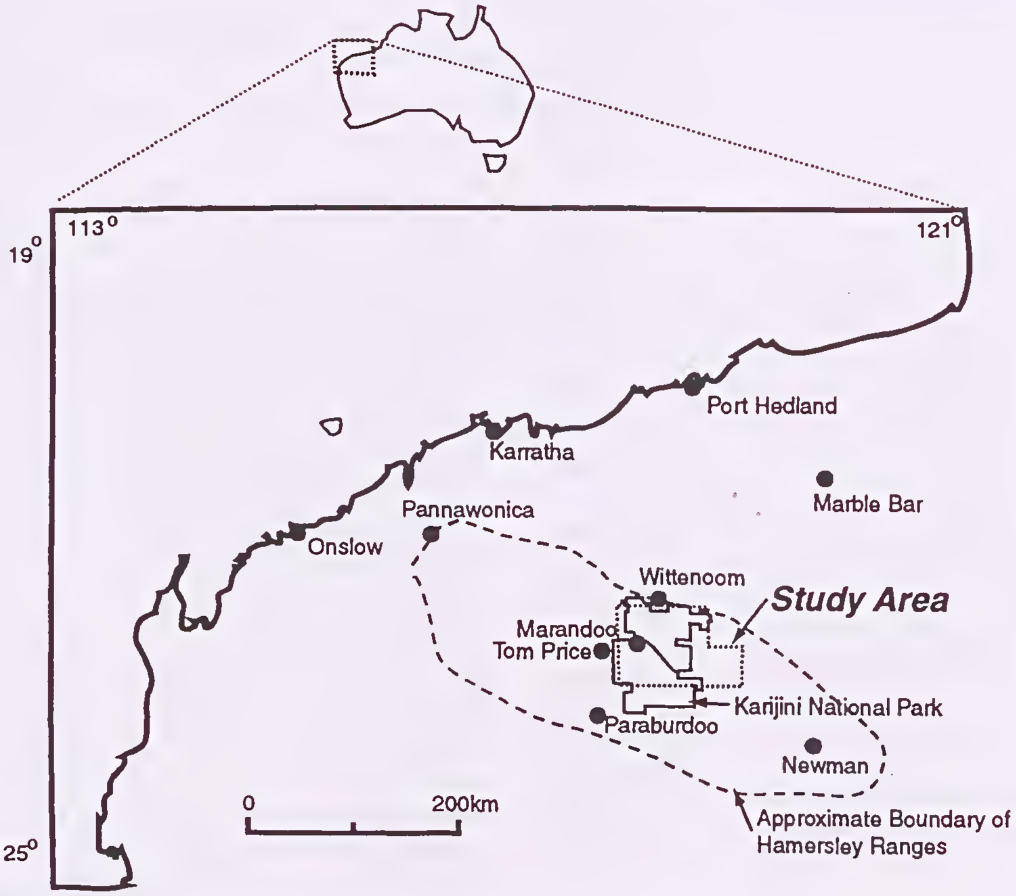

Figure 1. Location map showing the study area in relation to regional and State features.

found throughout the geological profile, particularly in the softer, dolomitic formations. The surface geology is therefore somewhat complex with the main geological formations of the study area surface being the Brockman Iron Formation, the older Marra Mamba Iron Formation, the Jerrinah Formation (very complex and dominated by dolomite and shale), the Weeli Wolli Formation (also dolomite and shale), Archaean granite, volcanics, Tertiary consolidated colluvium, the Oakover Formation (Tertiary calcareous gravels and limestone), Quaternary colluvium, and Quaternary alluvium (Thorne & Tyler 1997).

No long-term rainfall records are available for the study area. However, interpolation of long-term records from surrounding stations suggests rainfall for the study area is around 350 mm per annum on average (Beard 1975; van Etten 2000) and decreases in a southerly direction. This average figure however belies the very large temporal variability in rainfall across the region; the variability index of annual rainfall is between 1 and 1.2, which is classified as moderate to high (Bureau of Meteorology 1989). This variability mainly stems from the erratic nature of cyclonic rains during summer and autumn. In some years, cyclones cross the coast and bring large amounts of rain to the arid interior, whereas in other years no effective cyclonic rains may occur (Beard 1975). Winter rainfall averages around 40–50 mm, increases with distance south and is much more regular than summer rain. Temperatures and evaporation rates are high in summer with the mean January maximum close to 40°C. Winter maximum temperatures average around 24°C, with average minimum around 11°C. Mild frosts have regularly been observed during winter (Beard 1975), particularly in valleys and hollows.

Study sites & field measurements

Truly random selection of study sites was not possible given the lack of roads and tracks, the restrictions on off-road vehicle use and the ruggedness of the terrain. Alternatively, available roads and vehicle tracks were used to sample as much variation in landform type, geological substrate and altitude as possible. Altogether 139 sites were chosen for study. All major landform types and geological substrates were sampled several times throughout the study area. Areas immediately adjacent to roads were avoided because of the potential for edge effects, as were recently burnt areas given they have a suite of pioneer species. Sampling occurred over seven separate periods: June 1991, August 1991, December 1991, July 1993, December 1993, December 1994 and July 1995. The amount of rainfall before sampling, which influences annual and ephemeral species composition, varied considerably.

At each study site, a 20 m x 25 m plot was marked out on the ground and then divided into twenty 5 m x 5 m quadrats. This size plot (0.05 ha) was used as it has been recommended for studies of arid woodland communities (Fox 1981; Kent & Coker 1992) and supported by examination of species-area curves which showed they regularly capture the majority of species present at sites. In each 25m^2 quadrat, the abundance (number of individuals) and cover of each perennial species was estimated. Perennial species in this study included short-lived perennials (sometimes referred to as semi-perennials) which can survive longer than a year given favourable conditions. Most species of semi-perennials were present at all sampling times over the course of the study, although their abundance and the amount of green tissue varied somewhat. True annual species (i.e. those which consistently complete their life-cycles within a year) were not included in the analyses given their temporal variability. Species were identified using relevant keys and the W.A. Herbarium (Perth) collection with the authority for plant names and nomenclature being Paczkowska & Chapman (2000). Voucher specimens of all species collected are lodged in the Edith Cowan University Herbarium (Joondalup Campus).

Data analysis

An importance value (IV) was calculated for each perennial species at each plot by summing the relative cover, density and frequency of plants and multiplying by 100 (Curtis 1959). The sum of IVs for all species in a plot is 300. The IV of each species in the plot is therefore relative to the other species in the plot and is not an absolute measure. The main advantage of the importance value over other measures of cover/abundance is that it enables fair comparison of different sized plants. For instance a tree species (typically high cover, but low abundance) can have similar IVs to grasses/herbs/subshrubs (low cover, high abundance), but would differ considerably if either cover or abundance measures only were used. IVs were log transformed using the formula $x' = \log_e(x + 1)$ to downweight dominant species and to reduce the skewness of the data set – this effectively reduced the data to between 0.1 to 5. A site by species matrix was then constructed using transformed IVs and converted to a site X site dissimilarity matrix using the Bray-Curtis association measure (Bray & Curtis 1957) as recommended by Faith *et al.* (1987). Classification of sites was performed on the dissimilarity matrix using two different clustering strategies: ALOC (Belbin 1987) and flexible-UPGMA (Belbin *et al.* 1992). For the flexible version of UPGMA, b values of -0.1, as recommended by Belbin & McDonald (1993), were used. Ordination of the site dissimilarity matrix was performed using a hybrid multidimensional scaling method (SSH) with the "ratio-ordinal cut value" set at around 0.8 as suggested by locating a trough in the histogram of association values (Belbin 1991, 1994). In addition to ordination of all 139 sites, 35 sites located along a particular ridge-top to valley floor toposequence near Marandoo (Fig 1) were ordinated and a differential profile constructed by plotting the one-dimensional SSH scores against distance along topo-sequence (Hobbs 1986). Principal axis correlation (PCC) was used to calculate how well each species was linearly correlated to the ordination space and the direction of this correlation (Belbin 1994). To protect against spurious results using IV's, the same classification and ordination procedures were also undertaken using cover values (square root transformed) and compared to results using IV's.

Mean cover of all species and of various life-forms were compared for various vegetation units using one-way ANOVA, with Tukeys post-hoc test used to distinguish which pairs of means were significantly different. Means were first checked for equal variances and all cover values were arcsine transformed before analysis (Sokal & Rohlf 1981). Mean community species richness (of all species, as well as that of various life-forms), Shannon diversity index and evenness index (Kent & Coker 1992) were compared using Kruskal – Wallis test. Indicator species, defined as those species which characterise and differentiate a group, were determined for each community using the approach outlined by Dufrene & Legendre (1997). For each group of sites defined by the classifications, homogeneity (in terms of species composition) was calculated using the following formula: H=1-RV where *H* is the homogeneity and *RV* is the relative variance of a particular group and was calculated, following the recommendations of Pressey & Bedward (1991), using the dissimilarity measure used to construct the site X site association matrix. Simply, RV for a particular group was calculated as the average within-group association (i.e. of all pair-wise combinations of sites) divided by the average pair-wise association for the data set as a whole.

Results

Classification and descriptions of communities

The dendrogram resulting from the UPGMA classification of sites (Fig 2) was produced by first cutting the classification at the 21 group level and then joining 5 smaller groups (consisting of 1 or 2 sites) to adjacent groups in the dendrogram. This produced 16 groups,

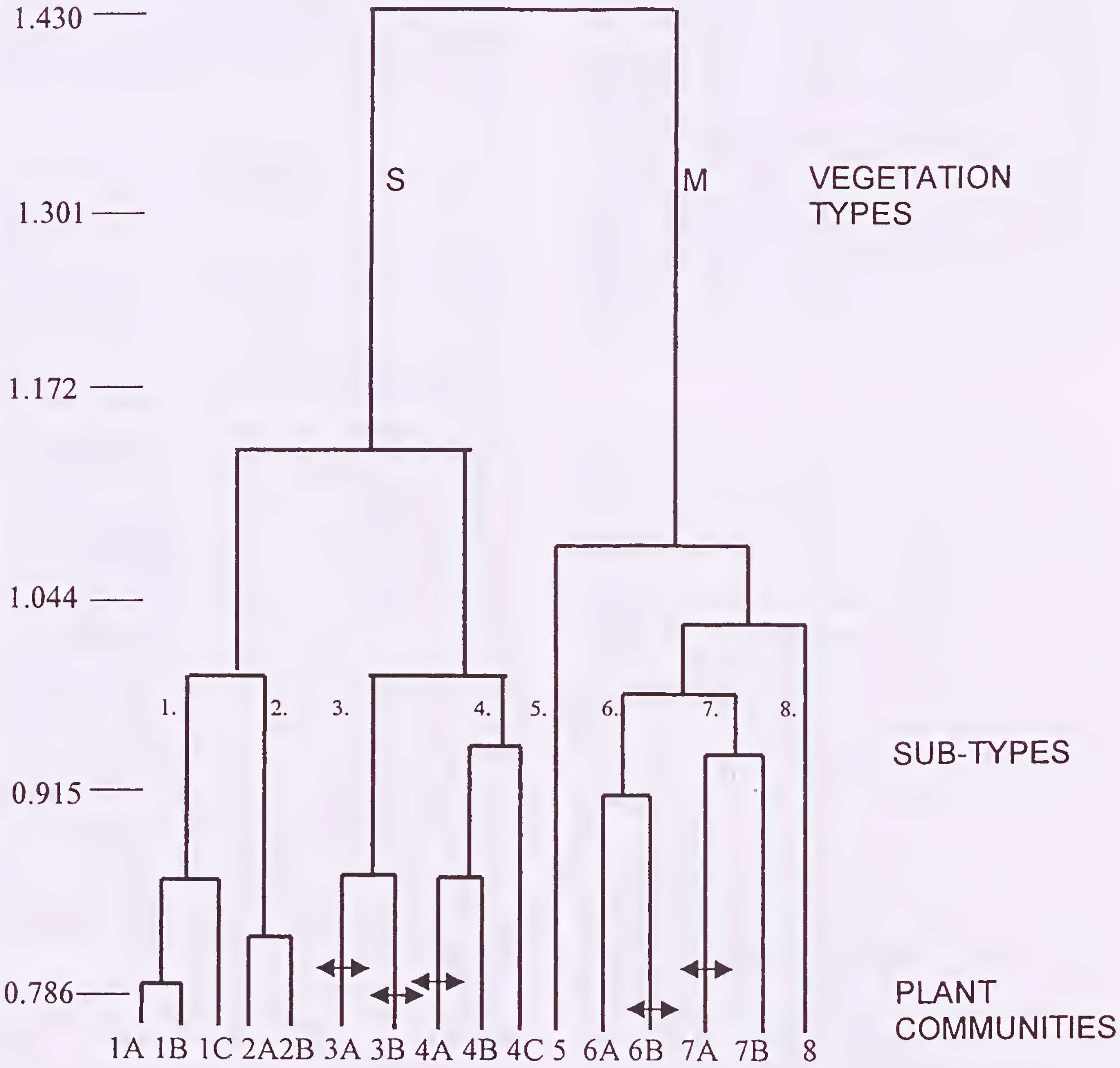

Figure 2. Partial dendrogram of the UPGMA classification of sites showing relationships between the 16 plant communities, 8 subtypes and 2 broad vegetation types. (N.B. The full dendrogram was originally cut at the 21 group level. Following fusion of adjacent groups, this number was reduced to 16. The positions of the original splits are shown on the dendrogram using arrows).

Table 1

Characterisation of plant communities in terms of dominant species in order of importance value (IV) with only species with IV of 5 or above listed. Key to genera as per text.

1A	1B	1C	2A
T. wiseana 96 *T. basedowii* 45 *T. brizoides* 27 *E. leucophloia* 21 *A. marramamba* 14 *S. g.* subsp. *pruinosa* 10 *T. pungens* 9 *A. atkinsiana* 8 *K. velutina* 7 *A. pruinocarpa* 7 *E. mucronata* 6 *A. maitlandii* 6 *S. g.* subsp. *glutinosa* 6	*T. basedowii* 117 *T. wiseana* 57 *E. leucophloia* 24 *A. adoxa* 19 *A. maitlandii* 12 *A. hilliana* 10 *C. hamersleyana* 7 *S. g.* subsp. *glutinosa* 5	*T. brizoides* 102 *E. leucophloia* 30 *T. wiseana* 23 *T. basedowii* 19 *S. g.* subsp. *glutinosa* 13 *A. maitlandii* 13 *E. mucronata* 9 *P. clementii* 8 *A. caricinus* 7 *Sida* aff. *filiformis* 5	*T. basedowii* 123 *E. gamophylla* 28 *T. wiseana* 24 *T. pungens* 19 *A. caricinus* 16 *A. contorta* 6 *S. a.* subsp. *oligophyllaX helmsii* 5
2B	**3A**	**3B**	**4A**
T. basedowii 196 *T. wiseana* 28 *E. leucophloia* 12 *A. stowardii* 8 *S. g.* subsp. *glutinosa* 6 *A. bivenosa* 5 *S. a.* subsp. *oligophylla X helmsii* 5	*T. wiseana* 117 *T. longiceps* 60 *E. trivalvis* 22 *M. eleuterostachya* 15 *E. socialis* 10 *Heliotropium* sp. 7	*T. wiseana* 93 *A. xiphophylla* 49 *T. longiceps* 32 *M. georgei* 16 *A. aneura* 15 *A. stowardii* 9 *S. a.* subsp. *artemisioides* 8 *A. victoriae* 8 *S. a.* subsp. *helmsii* 7 *Enneapogon caerulescens* 7 *Maireana* sp. #1 5	*T. wiseana* 128 *E. kingsmillii* 31 *A. caricinus* 14 *E. leucophloia* 11 *G. polyzygum* 9 *Goodenia stobbsiana* 8 *A. ancistrocarpa* 8 *Dampiera 'anonyma'* 7 *E. mucronata* 7 *T. bitextura* 6 *A. acradenia* 7 *O. xerophila* 5
4B	**4C**	**5**	**6A**
T. wiseana 188 *T. pungens* 18 *A. inaequilatera* 11 *E. leucophloia* 8 *A. bivenosa* 7 *S. enchinocarpa* 7 *P. rotundifolius* 6 *E. muconata* 6 *T. brizoides* 5 *S. g.* subsp. *glutinosa* 5 *P. obovatus* 5 *Petalostylis labicheoides* 5	*A. aneura* 77 *T. wiseana* 54 *D. viscosa* 17 *E. latrobei* 10 *E. muconata* 10 *A. ayersiana* 9 *T. triandra* 9 *P. obovatus* 9 *M. villosa* 8 *Sida* sp. #6 8 *A. rhodophloia* 6 *S. g.* subsp. *X luerssenii* 6 *S. viminale* 6 *R. eremaea* 6 *T. pungens* 5 *Erempohila* sp. #2 5 *S. g.* subsp. *glutinosa* 5	*T. melvillei* 149 *A. aneura* 44 *T. wiseana* 15 *A. pruinocarpa* 9 *C. deserticola* 7 *E. forrestii* 6 *Eragrostis dielsii* 5 *T. pungens* 5	*A. aneura* 36 *A. contorta* 29 *Mai. villosa* 20 *C. fallax* 19 *E. polyphyllus* 15 *T. triandra* 13 *T. pungens* 12 *A.* aff. *exonemum* 11 *E. aurea* 11 *E. 'lanceolata'* 10 *Sida fibulifera* 10 *Ab. otocarpum* 8 *E. caerulescens* 7 *E. xerothermica* 7 *E. victrix* 6 *P. clementii* 6 *P. obovatus* 6 *P. muelleri* 5
6B	**7A**	**7B**	**8**
A. aneura 85 *T. melvillei* 42 *C. fallax* 23 *T. triandra* 20 *P. obovatus* 19 *A. citrinoviridis* 6 *D. australasicus* 6 *E. 'lanceolata'* 5 *E. benthamii* 5	*T. triandra* 50 *E. aurea* 31 *T. pungens* 28 *E. xerothermica* 29 *T. wiseana* 25 *T. melvillei* 11 *A. dictyophleba* 7 *K. velutina* 6 *A. bivenosa* 5	*T. triandra* 51 *T. pungens* 27 *A. citrinoviridis* 30 *E. victrix* 18 *E. camaldulensis* 22 *D. forrestii* 9 *Porana commixta* 8 *E. benthamii* 7 *P. clementii* 6 *D. australasicus* 6 *I. monophylla* 6 *Sclerolaena cornishiana* 5 *S. lasiophyllum* 5 *A. bivenosa* 5	*E. aurea* 142 *A. aneura* 47 *E. victrix* 40 *M. florulenta* 33 *T. triandra* 8 *C. fallax* 7 *A. contorta* 7

hereafter referred to as *plant communities*. The dendrogram was also cut at the two group level to distinguish broad *vegetation types* (i.e., vegetation type 'S' and vegetation type 'M') and at the eight group level to distinguish *vegetation subtypes*. Although the determinations of cut levels and group unions were ultimately subjective, choices were guided by homogeneity analysis (i.e where average group homogeneity begins to plateau as more groups are defined by the classification; see Pressey & Bedward 1991; Bedward *et al.* 1992), the shape of the dendrogram (e.g. cuts occurred at distinct gaps in the hierarchy), and the desire to ensure that sites grouped together had a reasonable consistency in terms of dominant and common species.

The names and descriptions of the 2 vegetation types, 8 subtypes and 16 plant communities so derived follow. Dominant and indicator species for each community are shown in Tables 1 & 2, respectively.

Vegetation type 'S': hummock grassland with emergent trees & shrubs

This vegetation type dominates the upland ridges, hills and mountains as well as the pediment slopes. It is dominated by various species of hummock grasses of the genus *Triodia*, colloquially known as "spinifex" (Jacobs 1992). The genus is endemic to Australia and dominates large parts of the arid northern Australia. Hummock grasslands are rarely 'pure' grasslands as scattered trees and/or tall shrubs are usually present. Under some classification schemes (e.g. Specht 1981), these formations would be described as woodland or open woodland, but the term hummock grassland is preferred given the low cover of trees. In the study area, these trees and shrubs typically cover 5–10% and are chiefly of the genera *Eucalyptus*, *Acacia* and *Senna* (syn. *Cassia*). Hummock grasses themselves typically cover 20–25% of the soil surface.

Subtype 1: Hummock grassland with emergent *Eucalyptus leucophloia* on ridge, mountain and hill slopes

Community 1A: *Triodia wiseana – T. basedowii* hummock grassland with emergent *Eucalyptus leucophloia* and tall *Acacia* shrubs (on Marra mamba ridges and slopes; 9 sites).

T. wiseana dominates this community, but is often mixed with *T. basedowii*. *E. leucophloia* (snappy gum) is the dominant tree at around 5% cover. Tall *Acacia* shrubs and small trees such as *A. marramamba* (indicator species and seemingly restricted to this geological substrate), *A. atkinsiana* (also an indicator species), *A. maitlandii*, *A. pruinocarpa*, *A. hamersleyensis*, *A. pyrifolia* and, in places, *A. aneura s.l.* are scattered throughout and sometimes form distinctive groves along the contour on less steep slopes. Shrubs, including *Senna glutinosa* subsp. *pruinosa*, *S. glutinosa* subsp. *glutinosa* and *Keraudrenia velutina* subsp. *'elliptica'* ms, form a very sparse, low-shrub layer. Grasses such as *Eriachne mucronata*, *Eragrostis eriopoda* and *Paraneurachne muelleri* are occasionally found between the hummocks, but herbs and subshrubs are rarely found (Tables 1 & 3) except in the first 1–3 years following fire (pers. obs.).

Community 1B: *Triodia basedowii – T. wiseana* hummock grassland with emergent *Eucalyptus leucophloia*, *Corymbia hamersleyana* and low *Acacia* shrubs. (on Brockman ridges and slopes;13 sites).

This community is similar to community 1A in terms of structure and dominant species (although *T. basedowii* is often the most common species in the hummock grass mix). The major difference is the suite of shrubs present. Here small shrubs, such as *A. adoxa* and *A. hilliana*, dominate a sparse, low shrub layer (3–4% cover), with a tall shrub layer virtually absent (although *A. maitlandii* can be locally common). Another distinction from 1A is the bloodwood tree *C. hamersleyana* being a sparse but regular feature of the upper stratum. Subshrubs (small, predominantly non-woody shrubs such as *Sida* spp., *Stemodia grossa*, *Goodenia* spp.) are again uncommon in this community (Tables 1 & 3), yet are generally distinct from those of community 1A, with only one of twenty species common to both communities (namely *Abutilon otocarpum*).

Community 1C: *Triodia brizoides* hummock grassland with emergent *Eucalyptus leucophloia* (on shallow, skeletal soils on slopes and ridges; 7 sites)

Although also structurally similar to 1A, this community is dominated by *T. brizoides* (20–25% cover), a species which seems able to tolerate the shallow, skeletal soils found around outcrops of bedrock and on steeper slopes. Other perennial grasses such as *E. mucronata*, *Paspalidium clementii*, *Triodia bitextura* and *Amphipogon caricinus* are also present, particularly in the interstices of rocks and outcrops. Shrubs are less common than in communities 1A and 1B, the most common being *S. glutinosa* subsp. *glutinosa*, *A. maitlandii* and *Dodonaea coriacea* (the latter is an indicator species; Table 2).

Subtype 2: Hummock grassland of *Triodia basedowii* on pediment slopes.

Community 2A: *Triodia basedowii* hummock grassland with emergent *Eucalyptus gamophylla* mallee (on lower to middle pediment slopes; 17 sites).

The gentle pediment slopes (of around 1–3°) have shallow soils (20–30 cm deep) and are covered with small pebbles forming an ironstone pavement. Here the hummock grassland is dominated by *T. basedowii* and the mallee *E. gamophylla* is the dominant and characteristic emergent. No trees are found with the exception of *Hakea lorea* and *C. deserticola* at low densities. There is little development of a shrub layer (only ~2% cover) with the main species being the hybrid *Senna artemisioides* subsp. *oligophylla* x subsp. *helmsii*, *Bonamia rosea* and *Indigofera monophylla*. *Acacia* shrubs (such as *A. stowardii* and *A. ancistrocarpa*) occur but are relatively sparse. Semi-perennial grasses are fairly common between hummocks at some sites.

Community 2B: *Triodia basedowii* hummock grassland with emergent *Eucalyptus leucophloia* and mixed *Acacia* and *Senna* shrubs (on upper pediment slopes; 12 sites).

Again *T. basedowii* is the dominant hummock grass and species present. A very low density of *E. leucophloia* occurs mixed with leguminous shrubs and small trees

Table 2

Characterisation of plant communities in terms of indicator species in order of indicator value (%) as calculated using the procedure of Dufrene & Legendre (1997), with only species with indicator value above 15% or top ten listed.

1A	1B	1C	2A
A. marramamba 65 *S.g.*subsp.*pruinosa* 38 *A. atkinsiana* 36 *H. lorea* 20 *Eremophlia* aff.*compacta* 19 *K. velutina* 16 *E. leucophloia* 16 *A. hamersleyensis* 15 *H. coatsii* 15	*A. adoxa* 63 *A. hilliana* 50 *A. maitlandii* 26 *C.hamersleyana* 25 *T. basedowii* 22 *E. leucophloia* 17 Unknown sp#4 16 *Grevillea wickhamii* 15	*T. brizoides* 73 *D. coriacea* 43 *S.g.*subsp. *glutinosa* 28 *T. bitexura* 26 *E. leucophloia* 19 *Gossypium robinsonii* 16	*E. gamophylla* 56 *T. basedowii* 24 *Sclerolaena parvifolia* 24 *C. deserticola* 21 *B. rosea* 18
2B	**3A**	**3B**	**4A**
T. basedowii 39	*M.eleuterostachya* 67 *E. trivalvis* 67 *E. socialis* 56 *T. longiceps* 28 *Heliotropium* sp. 22 *A. victoriae* 19	*A. xiphophylla* 59 *E. cuneifolia* 57 *M. georgei* 51 *A. victoriae* 40 *Maireana* sp.#1 38 *Sida* aff.*kingii* 24 *E.caerulescens* 24 *Sclerolaena* sp.#1 20 *Eremophila* aff.*freelingii* 20 *Templetonia* aff.*egena* 20	*E. kingsmillii* 69 *G. polyzygum* 44 *A. acradenia* 40 *G. stobbsiana* 35 *A. caricinus* 28 *C. ambiguus* 23 *Corchorus* sp.'*Hamersley*' 20 *Acacia spondylophylla* 20 *Dampiera anonyma* 19 *O. xerophila* 18
4B	**4C**	**5**	**6A**
A. inaequilatera 22 *T. wiseana* 19 *P. rotundifolius* 15	*S. viminale* 78 *E. latrobei* 65 *D. viscosa* 60 *A. ayersiana* 30 *Cheilanthes lasiophylla* 30 *S.g.*subsp.*luerssenii* 25 *Psydrax suaveolens* 24 *R. eremaea* 24 *A. aneura* 24 *E. fraseri* 20	*T. melvillei* 70 *C. deserticola* 27 *R. linearis* 18 *E. forrestii* 16 *Psydrax attenuatum* 15 *A. pruinocarpa* 15	*A. otocarpum* 76 *A.contorta* 70 *E. polyphyllus* 59 *M. villosa* 58 *Convolvulus* aff.*remotus* 57 *A.* aff.*exonemum* 52 *S. fibulifera* 50 *Boerhavia* sp. 46 *Abutilon* sp.#1 43
6B	**7A**	**7B**	**8**
P. obovatus 31 *A. aneura* 27 *Maireana tomentosa* 26 *C. fallax* 25 *T. melvillei* 18 *Enchylaena tomentosa* 17 *Eragrostis falcata* 17 *D. australasicus* 15	*E. xerothermica* 52 *A. dictyophleba* 44 *A. validinervia* 31 *T .triandra* 30 *A. colei* 15	*E. camaldulensis* 98 *R. kempeana* 75 *A. citrinoviridis* 62 *S. cornishiana* 55 *D. forrestii* 50 *P. maderaspatensis* 50 *Evolvulus alsinoides* 45 *I. monophylla* 42 *T .triandra* 35 *P. labicheoides* 32	*M. florulenta* 96 *E. auraea* 82 *E. victrix* 57 *A. aneura* 15

such as *A. bivenosa*, *A. stowardii*, *S. artemisioides* subsp. *oligophylla* x subsp. *helmsii*, *A. pruinocarpa*, *A. ancistrocarpa* and *S. glutinosa* subsp. x *luerssenii*. These latter species occur in other communities, but are typically more common here. The species diversity is significantly lower here than in most other hummock grassland communities and the tree and shrub cover is relatively small (Table 3). Floristically and structurally, this community is intermediate between 1A/1B and 2A.

Subtype 3: Hummock grassland and mixed *Acacia* woodland on calcareous, alkaline soils.

Community 3A: *Triodia wiseana* – *T. longiceps* hummock grassland with emergent *Eucalyptus trivalvis* – *E. socialis* mallee (on Oakover and dolomite flats/undulating land; 9 sites).

This community comprises a mosaic of the two hummock grass species (again 20–25% total cover) with

Table 3

Comparison of plant communities in terms of mean species richness and diversity, mean homogeneity, and cover (%) for all perennial and semi-perennial species and for various life-forms. Standard errors in parentheses. Test statistics refer to results of one-way ANOVA or Kruskal-Wallis test. 'Outstanding' refers to communities which were significantly different from the majority of ther communities according to relevant pair-wise comparison test. Probability levels: *: $p<0.5$; ** $p<0.1$; ***:$p<0.001$. (# richness and diversity measures do not include annual species for reasons outlined in the text).

COMMUNITY	1A	1B	1C	2A	2B	3A	3B	4A	4B	4C	5	6A	6B	7A	7B	8	Test Stat.	Prob.	Outstanding
Species Richness#	16.7 (2.0)	14.2 (0.8)	17.7 (1.8)	15.0 (1.6)	9.4 (0.8)	12.3 (1.5)	13.6 (3.4)	14.7 (1.5)	14.2 (1.7)	18.3 (1.9)	12.6 (1.6)	32.6 (5.5)	15.9 (1.7)	18.4 (2.4)	32.3 (5.4)	5.5 (0.5)	c2=44.4	***	2B,6A,7B,8
Species Diversity#	0.84 (0.07)	0.77 (0.03)	0.87 (0.06)	0.83 (0.05)	0.54 (0.05)	0.69 (0.06)	0.85 (0.11)	0.84 (0.07)	0.70 (0.07)	1.00 (0.08)	0.71 (0.05)	1.21 (0.08)	0.87 (0.07)	0.91 (0.07)	1.24 (0.10)	0.48 (0.01)	c2=57.8	***	2B,6A,7B,8
Eveness Index#	0.65 (0.04)	0.64 (0.03)	0.66 (0.03)	0.64 (0.02)	0.51 (0.03)	0.61 (0.03)	0.72 (0.04)	0.68 (0.05)	0.59 (0.04)	0.78 (0.04)	0.60 (0.03)	0.82 (0.01)	0.72 (0.03)	0.70 (0.03)	0.81 (0.03)	0.65 (0.04)	c2=58.6	***	2B,6A,7B,4C
No. Rare Species#	0.4 (0.3)	0.4 (0.2)	1.2 (0.7)	0.5 (0.2)	0.08 (0.08)	1.7 (0.3)	2.0 (1.1)	3.5 (1.5)	0.8 (0.2)	1.6 (0.9)	0.4 (0.2)	2.4 (0.9)	1.7 (0.6)	1.4 (0.6)	4.3 (1.0)	0	c2=50.1	***	7B,4A,6A
No. Common Species#	13.0 (2.1)	11.3 (0.7)	12.1 (1.2)	12.7 (0.9)	8.4 (0.9)	5.4 (1.0)	7.8 (1.1)	7.8 (0.9)	9.9 (1.2)	9.2 (1.3)	7.8 (0.9)	14.3 (1.8)	8.0 (1.2)	10.1 (1.2)	11.5 (1.3)	2.5 (0)	c2=63.1	***	6A,2A,1A,1C
Total Cover	35.3 (2.9)	37.5 (2.5)	35.3 (1.7)	28.2 (2.0)	29.6 (4.1)	30.3 (4.5)	24.3 (4.0)	22.3 (3.9)	37.7 (2.3)	37.2 (3.7)	27.1 (2.9)	48.5 (9.9)	27.6 (4.8)	42.0 (4.5)	42.0 (9.0)	32.1 (4.0)	*F*=2.7	**	6A, 7A
Tree Cover	5.0 (2.0)	5.7 (0.5)	7.3 (1.2)	5.5 (0.7)	3.8 (1.4)	5.8 (2.1)	11.3 (3.0)	7.3 (1.7)	2.7 (0.8)	23.9 (4.4)	6.5 (0.9)	15.2 (3.5)	16.3 (3.8)	9.1 (3.1)	17.4 (3.8)	17.5 (9.4)	*F*=6.5	***	4C,6B,6A,7B,4B
Shrub Cover	4.0 (0.7)	4.2 (0.8)	2.7 (0.5)	2.0 (0.6)	1.2 (0.2)	2.6 (0.4)	2.5 (0.9)	4.2 (0.9)	1.2 (0.3)	5.1 (1.1)	1.7 (0.4)	2.5 (0.6)	1.6 (0.6)	3.2 (1.2)	5.1 (4.0)	3.2 (2.8)	*F*=1.8	ns	nil
Herb/Subshrub Cover	0.5 (0.1)	0.5 (0.1)	0.9 (0.3)	0.8 (0.1)	0.24 (0.08)	0.8 (0.2)	1.3 (0.6)	1.2 (0.7)	0.9 (0.3)	3.6 (1.0)	0.6 (0.1)	13.0 (5.0)	2.2 (0.8)	1.4 (0.5)	3.6 (1.0)	1.2 (0.05)	*F*=8.5	***	6A,4C
Creeper/Climber Cover	0.4 (0.2)	0.2 (0.1)	0.2 (0.1)	0.9 (0.3)	0.2 (0.1)	1.7 (1.1)	0.2 (0.1)	0.2 (0.1)	0.4 (0.2)	2.0 (0.4)	0.9 (0.3)	2.0 (0.8)	1.5 (0.7)	1.3 (0.6)	2.9 (0.4)	0	*F*=2.0	ns	nil
Succulent Cover	0.3 (0.2)	0	0.7 (0.3)	0.3 (0.2)	0	1.2 (0.9)	3.2 (1.8)	0	0.1 (0.07)	3.6 (1.9)	0.8 (0.5)	5.1 (2.0)	1.4 (0.6)	0.2 (0.1)	2.2 (0.8)	0	*F*=7.2	***	3B,4C,6A,7B
Grass Cover	25.9 (2.6)	27.1 (1.9)	24.3 (1.8)	20.1 (1.4)	24.7 (3.5)	21.7 (4.1)	9.2 (2.6)	9.7 (2.3)	32.5 (5.4)	4.6 (1.1)	19.0 (2.2)	17.6 (4.0)	7.6 (3.3)	26.7 (2.9)	16.2 (6.5)	11.5 (3.7)	*F*=6.8	***	6B,4C,3B,4A,4B
Homogeneity	0.33	0.37	0.24	0.24	0.33	0.16	0.17	0.24	0.20	0.24	0.25	0.28	0.21	0.15	0.28	0.73	–	–	–
No. of Sites	9	13	7	17	12	9	5	7	8	5	13	7	12	8	4	2	–	–	–

emergent and characteristic mallee eucalypts such as *E. trivalvis*, *E. socialis* and, less commonly, *E. repullulans*. Average mallee cover is around 5%. *Melaleuca eleuterostachya* is by far the most common and characteristic shrub species present, with others such as *Heliotropium* sp. and *A. bivenosa* also found. This community was found on basic soils derived from calcareous parent rocks of the tertiary Oakover formation and older dolomites and shales such as those which predominate on the Jerrinah formation.

Community 3B: *Triodia wiseana* hummock grassland with emergent *Acacia xiphophylla* and other *Acacia* spp. (on dolomitic and volcanic slopes and ridges; 5 sites).

As with 3A, *T. wiseana* dominates this community. However the distribution of the grass is more patchy here as it gives way to relatively dense stands of *A. xiphophylla* (snakewood) and other acacias such as *A. stowardii*, *A. victoriae* and *A. aneura*. Dense stands of *A. xiphophylla* typically occur below major outcrops of calcrete bedrocks (breakaways) and are often mixed with *A. aneura*. The other acacias are found on more gentle slopes where the vegetation also typically contains numerous chenopod species, particularly of the genera *Maireana* and *Sclerolaena*. Considerable site to site variation in species composition was evident within this community with low homogeneity recorded (Table 3). Indicator species in addition to *A. xiphophylla* include *Eremophila cuneifolia*, *M. georgeii* and *A. victoriae* (Table 2). This community was found predominantly in the south-west of the study area where the geology and topography is more complex than elsewhere and includes outcrops of and soils derived from dolomites, dolerites, quartzites, basalts, shales and cherts, and sandstones. Further sampling of this community type is recommended to determine if it should be divided into 2 types: 1) snakewood woodland on slopes below calcrete outcrops; and 2) mixed *Acacia* and chenopod shrubland on very alkaline soils.

Subtype 4: Hummock grassland of *Triodia wiseana* with *Acacia aneura* or no/few emergent trees on a range of upland soils and landforms.

Community 4A: *Triodia wiseana* hummock grassland with emergent *Eucalyptus kingsmillii* low mallee (on mountain tops; 7 sites).

Eucalyptus kingsmillii is a small mallee characteristic of the summits of tall mountains of the Hamersley Ranges. Almost all mountain tops above approximately 1000 m have this community and it is rarely found at lower altitudes. *T. wiseana* is dominant, although *T. bitextura* is common at one site. Other eucalypts, such as *E. leucophloia* and *E. ewartiana* are found, but are sparse. Other common species vary with location; *Acacia acradenia*, *Gompholobium polyzygum*, *A. ancistrocarpa*, *Olearia xerophila* and *Hibbertia glaberrima* are examples of locally common indicator shrubs (Table 2). *Callitris glaucophylla* (cypress pine) is a fire sensitive tree found on steep slopes and other fire-excluded sites and is relatively common around mountain summits.

Community 4B: *Triodia wiseana* hummock grassland with emergent, sparse *Acacia inaequilatera* and *Eucalyptus leucophloia* (on volcanic formations; 8 sites).

This is another community dominated by the hummock grass *T. wiseana*. This community forms largely treeless hummock grassland; it has the lowest tree cover of all communities (Table 3). Trees, where present, are very sparse, with *A. inaequilatera* being the most widespread and common with an average of only 1.1% cover. In some areas very sparse *E. leucophloia* trees also occur. The shrub layer is also sparse and mainly consists of acacias such as *A. bivenosa*, *A. tetragonophylla* and *A. stowardii* and subshrubs such as *Ptilotus obovatus*, *P. rotundifolius*, *Sida echinocarpa* and *Solanum lasiophyllum*. This community was mostly found on extensive volcanic plains. Volcanic formations of the study area are varied and include dolerite intrusions (such as the Weeli-Wooli formation) to more extensive areas of older (Archaean) basalts. Where outcropping of the volcanic rock is marked, other perennial grasses (particularly *T. pungens*, *Cymbopogon ambiguus* and *Themeda triandra*) are typically found in the interstices of rocks and boulders together with more specialised species such as *Brachychiton gregorii*, *Hibiscus* aff. *coatsii* and *H. sturtii*. Two sites not on volcanics were classified in this community probably because they were dominated by *T. wiseana*. These were a mountain top site (without the usual *E. kingsmillii*, but with low density of *E. leucophloia*) and a site on calcareous soils of the Jerrinah formation with scattered *A. bivenosa* shrubs.

Community 4C: *Acacia aneura* woodland over *Triodia wiseana* hummock grass (on steep, scree slopes; 5 sites).

This community comprises dense stands of *A. aneura* (20–30% cover) over patchy *T. wiseana* and other perennial grasses such as *T. triandra* and *E. mucronata*. Broad leaved mulga (*A. ayersiana)* is also found. Subshrubs such as *P. obovatus*, *Maireana villosa*, *Rhagodia eremaea* and *Sida* spp. are relatively common. A range of indicator shrub species is also found, including *Eremophila latrobei*, *Dodonaea viscosa*, *Sarcostemma viminale* subsp. *australe* and *A. rhodophloia* (Table 2). This community is found on the steeper slopes of mountains and ridges where scree of ironstone formation covers the surface.

Vegetation type 'M': mulga woodlands with grassy understorey on alluvial flats, fans and drainage lines.

Mulga (*Acacia aneura s.l.*) dominates many of the plant communities of the valley systems within the Hamersley Ranges and is found, albeit at lower densities, in most of the other communities in low-lying areas. These areas typically feature the accumulation of fine alluvial soils washed down from the surrounding mountains and hills. Mulga woodlands are common vegetation types across the southern half of Australia's arid/semi-arid zones. *A. aneura* reaches its northern limit just north of the Hamersley Ranges (Beard 1975).

Community 5 (also *Subtype 5*): *Triodia melvillei* hummock grassland with emergent *Acacia aneura* (on upper to mid bajada slopes; 13 sites).

This community is characterised by dense hummock grass (*T. melvillei*) under a patchy stratum of *A. aneura* trees/shrubs. The density and cover of mulga is highly variable, but averages around 5–6%. Research in the study area (e.g. Start 1986; van Leeuwen *et al.* 1995) and personal observations suggest that this density is controlled by fire, with the relatively fire-sensitive mulga increasing in density with time without fire. Structurally, therefore, this community varies from a hummock grassland (with emergent mulga) to an open woodland of mulga. Other reasonably common tree and shrub species include: *A. pruinocarpa*, *Eremophila forrestii* and *C. deserticola*. This community occurs on the very slight slopes of the bajadas and other areas of alluvial fans. The soils are relatively shallow (20–40cm deep) and are reported to be underlain by a siliceous hardpan (Lorimer 1991).

Subtype 6: Woodland of *Acacia aneura* on broad drainage flats and lines.

Community 6A: *Acacia aneura* woodland/open woodland with tussock grass understorey (on alluvial flats and broad drainage lines; 7 sites).

The woodland is relatively dense (> 15% cover) and is dominated by mulga, although it is sometimes mixed with sparse eucalypts such as *E. victrix* (on broad alluvial flats and basins) and *E. xerothermica* (on broad drainage lines). Tussock and bunch grasses, most of which are perennial, dominate the ground layer. Typically many grass species are found at each site, with the number increasing following large rainfall events. Examples of tussock grass include *Chrysopogon fallax*, *T. triandra*, *P. muelleri* and *Eulalia aurea*. Subshrubs are also common and average 13% coverage. Common subshrubs include *M. villosa*, *Abutilon* aff. *exonemum*, *A. otocarpum*, *Erempohila 'lanceolata'* ms (low woody shrub), *P .obovatus and Rhagodia eremaea*. Many of these have high indicator values (Table 2). Species richness and diversity are significantly higher than in most other communities, as are numbers of common and uncommon species (Table 3).

Community 6B: *Acacia aneura* woodland/open woodland with *Triodia melvillei* – tussock grass_understorey (on outwash plains, lower bajadas and broad drainage lines; 12 sites).

This community is similar in several respects to 6A; the main differences being the dominance of hummock grass (*T. melvillei*) in the ground layer and the occurrence of *A. citrinoviridis* and *A. pruinocarpa* in the tree layer. The community is typically found on lower parts of bajadas and outwash fans. The community appears floristically and structurally intermediate between types 5 and 6A and may well represent a transitional zone or ecotone between them. On extensive outwash plains this community often exhibits a grove-intergrove vegetation pattern (Mabbutt & Fanning 1987), known in other countries as tiger bush or vegetation arcs.

Subtype 6: Woodland of *Eucalyptus* spp. on confined drainage lines.

Community 7A: *Eucalyptus xerothermica* open woodland with *Themeda triandra – Eulalia aurea / Triodia pungens* understorey (within drainage lines; 10 sites).

Scattered *E. xerothermica* trees of 5–10% cover characterise the overstorey of this community, with the occasional *Corymbia semiclara*, *A. aneura* and *E. victrix* also found. It is typically found within distinct drainage lines on subdued topographies. The understorey typically consists of either a mix of two tussock grasses (*T. triandra* and *E. aurea*) or open hummock grasses (*T. pungens* and, less commonly, *T. wiseana*). Where hummock grasses dominate, tree cover is appreciably lower. Such sites also form a distinct group in the classification. Several indicator species occur in the shrub layer; these include *Acacia dictyophleba*, *A. colei* and *A. validinervia*

Community 7B: *Eucalyptus victrix – E. camaldulensis – Acacia citrinoviridis* woodland with *Themeda triandra – Triodia pungens* grassy understorey (along major creeklines; 4 sites).

A mixture of *E. victrix* (coolabah) and *E. camaldulensis* (river redgum) form a tall woodland formation along the major creeklines of the study area. *A. citrinoviridis* is another relatively common tree in these areas. The ground layer is dominated by perennial grasses such as *T. triandra*, *T. pungens* and, to a lesser extent, *Eriachne benthamii*, *E. mucronata*, *P. clementii* and *P. muelleri*. Shrubs comprise around 5% cover. A large number of shrub species were found in this community; the more common ones are *Dicladanthera forrestii* (indicator species), *Dipteracanthus australasicus*, *A. bivenosa*, *A. pyrifolia*, *A. sclerosperma*, *Solanum lasiophyllum* and *I. monophylla*. Several other indicator species identified for this community include *Rulingia kempeana*, *Phyllanthus maderaspatensis* and *Dodonaea lanceolata*. Overall species richness and diversity is significantly higher than at most other sites (Table 3).

Community 8 (also Subtype 8): *Eucalyptus victrix – Acacia aneura* open woodland over perennial tussock and bunch grasses (in broad drainage basins; 2 sites).

There are several internal drainage basins in the study area which collect water and sediment from the surrounding hills and ranges. Where the basin is extensive, an open woodland of coolabah (*E. victrix*), variously mixed with smaller mulga trees (*A. aneura*), is found on the very fine, deep alluvium at the lowest parts of the basin. This community is floristically poor (Table 3) with only tussock grasses (such as *E. aurea*, *T. triandra*, *C. fallax)*, bunch grasses (such as *A. contorta*) and the woody, much-branched shrub *Muehlenbeckia florulenta* (a characteristic species) being recorded in the understorey. As this community was only sampled in the middle of a dry period, the species richness recorded is likely to be below its potential maximum. This community is the most distinct in floristic terms (Fig 2).

The non-hierarchical classification procedure (ALOC; Belbin 1987), when forced to produce 16 groups, resulted in more-or-less the same groups, each with a very similar (sometimes identical) composition of sites to the groups resulting from the hierarchical procedure (UPGMA). The major differences between the two classifications were that ALOC: 1) divided the *T. wiseana/T. basedowii* hummock grasslands on slopes into upper slope/plateau sites and lower slope sites rather than into groups linked to geological substrate; 2) community 3B was divided into two groups, one dominated by *A. xiphophylla* and the other dominated by *A. victoriae* and chenopods; and, 3) the two coolabah-mulga woodland sites of the drainage basins (community 8) were clumped with mulga woodlands with bunch grasses (community 6A). These two coolabah-mulga sites had the lowest affinities to their group of all sites and indeed formed a separate group when the ALOC procedure was forced to produce 17 groups.

Classifications using an initial matrix of transformed species cover values rather than IVs also resulted in very similar groupings of sites to that described above, and, for most communities, their composition in terms of sites were identical. The two major differences of the dendrogram produced using cover values were: 1) community 4B contained several more sites dominated by *T. wiseana* including several which were not on volcanic plains but on hill tops and upper slopes of Brockman ironstone formation where several of the characteristic shrubs of this formation are often absent; and 2) community 7A was more clearly divided into two groups, one with the ground-layer dominated by *T. pungens* and the other by *T. triandra* and other tussock grasses. This synchrony between the two classification approaches is no doubt derived from the strong correlation between transformed IVs and cover values (r=0.87; n=190).

Analysis of similarity (ANOSIM) test, performed with 1000 random permutations, demonstrated that the 16 groups determined by the two classification procedures were always more dissimilar to each other than 16 groups randomly determined. This implies that groups determined are significantly different to one another in terms of species composition (p<0.001). Although this is expected, the ANOSIM, and the fact that two completely different classification algorithms (one hierarchical and the other not) produced very similar groupings, support the idea that "real" groupings were detected and suggest that correct decisions were made with respect to classification methodology (Belbin 1994).

Community comparisons

A comparison of structural, floristic and growth-form features are displayed in Table 3 for the plant communities. There are several significant structural differences between the various plant communities and vegetation types. Mean total cover varies from 22% on mountain tops to 42–50% on drainage lines and flats. Mulga woodland on flats (community 6A) and *E. xerothermica* woodland within drainage lines (7A) have significantly higher cover than hummock grassland communities (Table 3). Tree cover is, not surprisingly, significantly higher in woodland communities compared to communities of hummock grassland on slopes and pediments (typically 15–24% cover compared to between 4–6% cover of trees). Tree cover on volcanics (community 4B) is significantly lower on average than many other communities, including some hummock grassland ones. Grass cover is relatively high (20–30%), except in the following communities which are significantly lower than most others: mulga woodland on scree slopes (4C), snakewood woodlands (3B), hummock grassland on mountain tops (4A) and mulga – *T. melvillei* – tussock grass (6B).

Average (perennial) species richness and diversity are significantly higher within mulga woodland on flats (community 6A) and creekline *E. camaldulensis* – *E. victrix* woodlands (7B) than in most other communities (Table 3). In addition, far more annual/ephemeral species were sampled in plots of these two communities than in hummock grassland communities. Hummock grassland on pediments and bajada slopes (communities 2A, 2B & 5) are generally less rich and diverse than other communities. Community 8 (*E. victrix* woodland of alluvial basins) had the lowest perennial richness and diversity of all communities (Table 3); median values were significantly lower than most other communities. Diversity values, although heavily influenced by species richness, also depend on the evenness of species distribution at sites. Values of evenness are relatively similar for all communities (i.e. around 0.6–0.7), except for communities 6A and 7B which are significantly higher (i.e. more even distribution of species) and 2B which is significantly lower than most other communities (Table 3). The richness of uncommon species (those found at less than 3 sites) is significantly higher (on average) within mulga woodland on flats (community 6A), along creeklines (community 7B) and on mountain tops (community 4A) compared to many other communities (Table 3). Whilst actual numbers would depend to a certain degree on the intensity of sampling in each community, these three communities have far more uncommon species than other similarly sampled communities. The uncommon species are mainly herbs and subshrubs in the first two communities, whilst they are mostly low shrubs on the mountain tops. Species positively identified as being rare and/or poorly known (as listed by the Western Australian Department of Conservation and Land Management) were few and mainly found on mountain tops.

Communities on calcareous soils (3A & 3B), *T. wiseana* hummock grassland on volcanics (4B) and *E. xerothermica* drainage line community (7A) are much less homogeneous in terms of species composition than other communities (Table 3). Each of these communities has at least one site that is distinct in some way to all the others. For instance, community 4B includes one site containing no trees on calcareous soils which seems to be placed in this group because of shared dominance by *T. wiseana*. Community 3B includes two quite dissimilar sites dominated by *A. victoriae* and other *Acacia* shrubs, rather than *A. xiphophylla*. They are clumped with other 3B sites because of understorey similarities. Quite possibly, these four heterogeneous communities will be split into a number of quite distinctive sub-communities, given the patterns shown in the classification, but sampling has been insufficient to confirm this. Communities which were relatively homogeneous in terms of species composition are 8, 1A, 1B and 2B (Table 3).

Ordinations of sites

The three-dimensional solution provided a considerable improvement in stress over a two dimensional solution (0.18 *c.f.* 0.26) and were hence used despite the increased difficulty in displaying patterns (Fig 3). Kruskal (1964) suggests that stress values less than 0.2 should be aimed for, whilst values less than 0.1 provide a "satisfactory" goodness of fit. These however are general guidelines at best as stress values are influenced by, amongst other things, number of sites and heterogeneity of communities. Ordinations performed using cover values rather than IVs in the initial site by site matrix produced a very similar pattern of

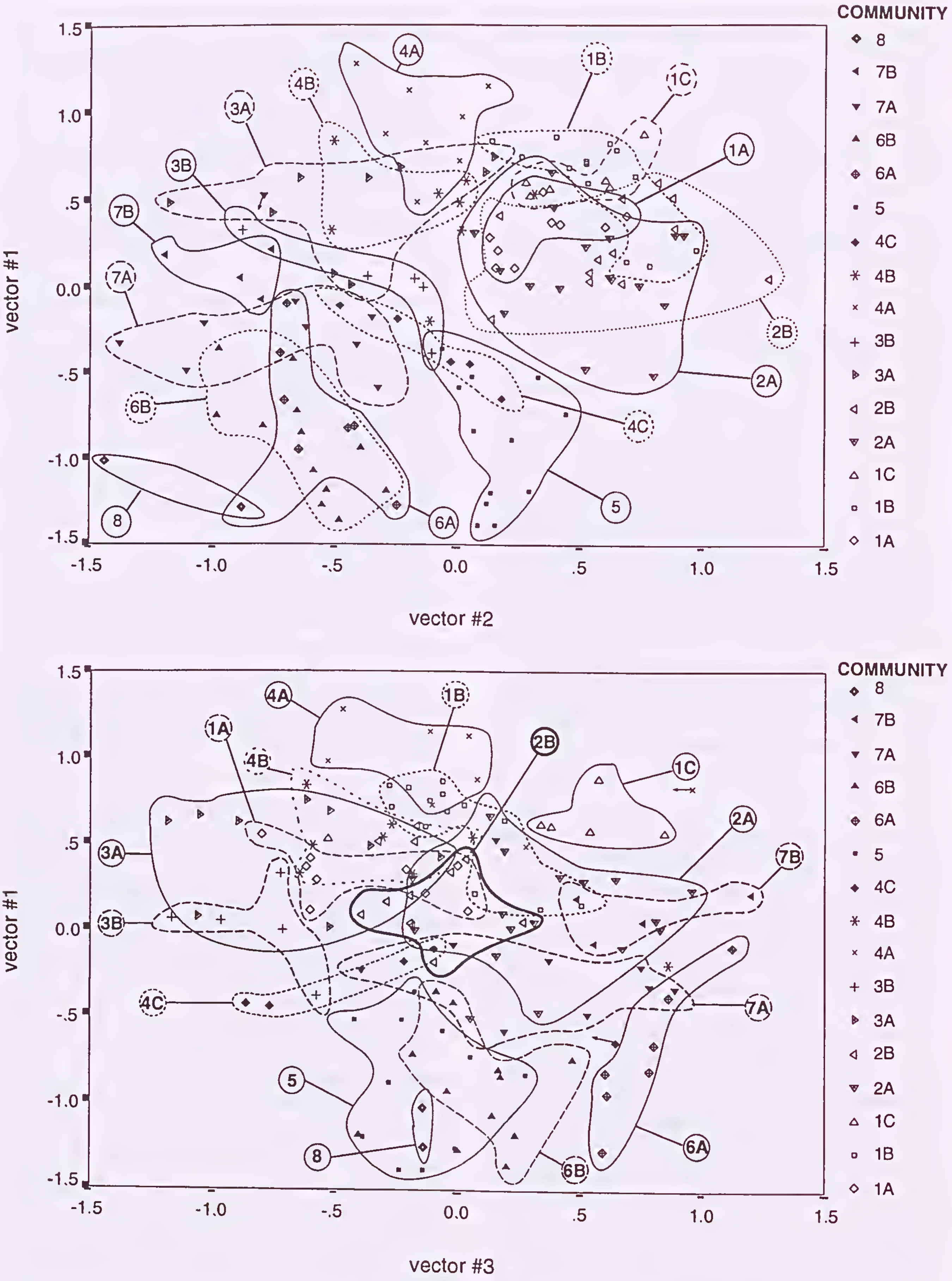

Figure 3. A 3-dimensional ordination of all sites based on all species and using SSH-MDS with the approximate space occupied by the 16 plant communities delineated: a) vectors 1 vs 2; b) vectors 1 vs 3.

communities. Procrustes rotation between the two ordinations demonstrated a very good level of fit (0.15) given the number of sites (Belbin 1994), indicating very little difference in general patterns displayed between using cover values and IVs as the initial data.

The three-dimensional ordination of all sites is displayed as two separate 2-dimensional plots (Fig 3). Sites belonging to a certain plant community generally grouped together in the ordination. Despite this general trend, the two outstanding features of the ordination plots were: 1) the considerable spread of sites within each community (reflects relatively high variability in species composition between sites within a plant community); and 2) the overlap of the ordination space occupied by a particular community with that of other communities. In other words, few discrete communities occurred. Indeed, a small number of communities clearly graded into other communities. There was also a small number of outliers (sites which are placed some distance from their respective community).

Hummock grassland at upland sites (communities 1A, 1B, 1C, 4A, 4B) were separated from the lowland communities more or less along the first vector (Fig 3). Generally the sequence of communities along this vector reflected topographic position with the mountain top community (4A) uppermost, followed by other upland communities, then pediment and bajada communities, with lowland communities at the base of this vector. Species strongly and significantly correlated to this vector were *A. aneura* (r = -0.79), *T. basedowii* (+0.74), *E. leucophloia* (+0.70), *T. triandra* (-0.67), *C. fallax* (-0.62), *E. xerothermica* (-0.51), *A. adoxa* (+0.47), *S. glutinosa* subsp. *glutinosa* (+0.41), *E. victrix* (-0.40), *M. villosa* (-0.39), *E. 'lanceolata'* (-0.36), *E. benthamii* (-0.36), *R. eremaea* (-0.36) and *C. hamersleyana* (+0.35). Of the upland communities, 1A, 1B & 1C were reasonably separate from each other along the first and third vectors (Fig 3b), however community 4B was highly variable and overlapped with each of these communities (Fig 3b), as well as communities 3A & 3B (Fig 3a). Community 4A (*E. kingsmillii* low mallee over hummock grass on mountain tops) formed a fairly distinct group along the first vector, but showed considerable variation along the third vector where it overlapped with communities 4B, 1B and 1C. The slight overlap with 1C was most likely by virtue of site E104 which is a mountain top site dominated by *T. brizoides* rather than *T. wiseana*, as is typical of community 4A. Pediment communities (2A and 2B) were not readily discernible from one another, were extremely variable and overlapped considerably with hummock grassland communities of uplands. They occupied the ordination space between the upland hummock grassland communities and the woodland communities on flats and other drainage features, although there was appreciably less overlap with the lowland communities (Fig 3). 2B was generally positioned between 2A and upland sites.

Communities on volcanics and calcareous soils (3A, 3B & 4B) were generally separated from those derived from ironstone formations along vector 3 (Fig 3b). Hummock grassland with mallee (community 3A) formed a distinguishable, albeit variable, group at the left of the plots (Fig 3). This group overlapped considerably with the community 4B group; both groups shared a dominance of *T. wiseana*, but have different dominant trees. Community 4B therefore occupied the ordination space between the calcareous and iron-formation hummock grasslands. The snakewood woodland community on calcareous soils (community 3B) formed a more discrete and less variable group than 3A, although there was some overlap.

In terms of lowlands, community 6B (mulga woodland with mixed *T. melvillei* and tussock grass understorey) occupied the ordination space between communities 5 (bajada mulga with *T. melvillei*) and 6A (mulga with tussock grass), and overlapped slightly with both (Fig 3). Mulga woodland on steep scree slopes (community 4C) formed a fairly discrete and confined group in the middle of the ordination space between the other mulga woodland communities and hummock grassland communities dominated by *T. wiseana*. The two drainage line communities (7A & 7B) separated along the first vector (Fig 3a). Community 7A overlapped considerably with mulga woodland communities, while 7B overlapped more with hummock grassland on calcareous and volcanic soils (3A & 3B; Fig 3a), as well as community 2A (Fig 3b). Sites on drainage and creek-lines seemed to be placed (in the ordination space) near to the communities which they abut in real (i.e. geographic) space. Community 8 (*E. victrix* woodland in broad drainage basins) formed the most distinct group, although it was placed near mulga woodlands.

Differential profile

The distributions of communities along the Marandoo topo-sequence are shown in the differential profile (Fig 4) with the degree of overlap between adjacent communities demonstrated in terms of species composition (vertical axis) and geographic distance (horizontal axis). A major change in species composition occurs between community 5 (*T. melvillei* hummock grassland) and communities 2A/2B (*T. basedowii* hummock grassland). The transition between 1A and 2A/2B was considerably more gradual both spatially and floristically, whilst that between 5 and 6B was relatively sharp, although it involved only a small degree of change in species composition (Fig 4). Other transitions were difficult to describe given inadequate sampling in and around the transition zones.

Discussion

This paper identifies and describes 16 plant communities within an approximately 8,000 km^2 section of the central Hamersley Ranges. Indicator species are also identified for each community. A small number of communities are distinct in terms of floristic composition, structure, species richness and diversity, whilst most are only subtly different and intergrade with other communities in respect of these parameters. The pattern of species distribution across the landscape is one of several dominant to sub-dominant species found across a wide range of communities (such as *T. wiseana*, *T. basedowii*, *A. aneura*, *E. leucophloia*, *S. glutinosa*, *P. obovatus*), with many of the other species uncommon and restricted to one or a few communities. A similar pattern of species distribution has been found in other mountainous deserts, such as Turkana, Northern Kenya (Patten & Ellis 1995), Oman (Ghazanfar 1991), central

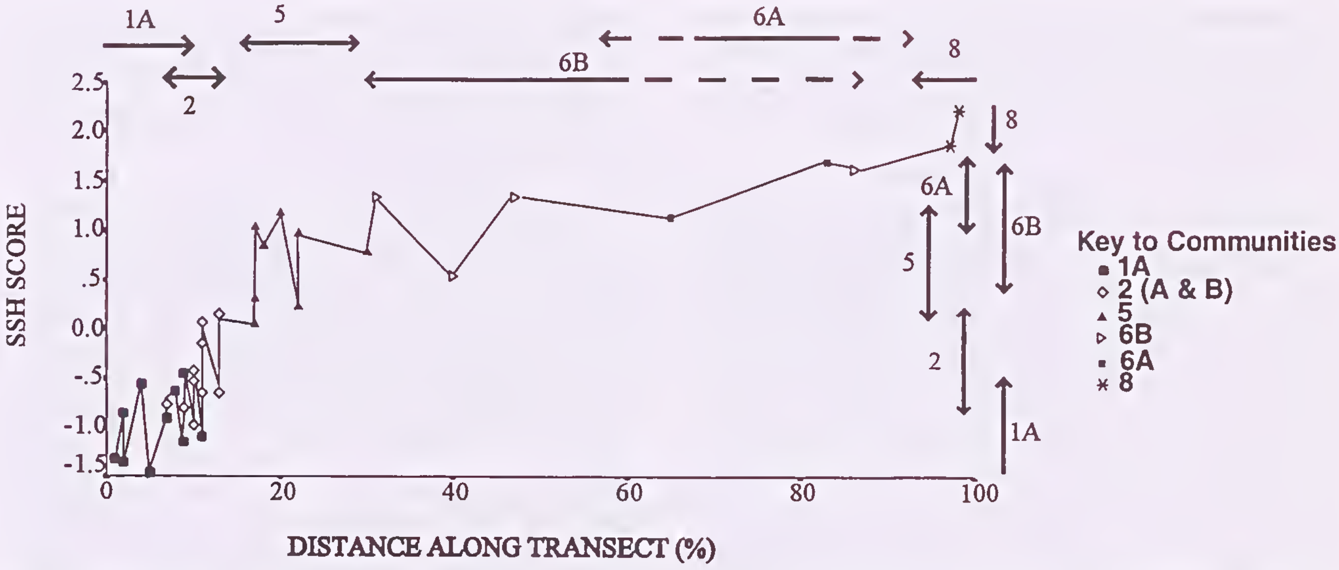

Figure 4. Differential profile showing changes in floristic composition (SSH score) with distance along a topographic profile of 35 sites located along a ridge top to valley floor catena at Marandoo. The approximate position of communities are indicated in both geographic space (horizontal axis) and ordination space (vertical axis).

Australia (Griffin 1990) and the Chihuahuan Desert of North America (Wierenga *et al.* 1987; Plumb 1991). Keighery *et al.* (2000) found certain *Acacia* species (such as *A. sclerosperma*, *A. tetragonophylla* and *A. linophylla*) widespread and often dominant across a range of vegetation types on red sands of the southern Carnarvon Basin. Similarly *A. aneura* dominates many recognisable plant communities in the Murchison River catchment (Curry *et al.* 1994).

Nine types of hummock grassland communities are identified on upland and piedmont slopes. These communities have very uneven species distributions as the hummock grasses (mostly either one or two of *T. wiseana*, *T.basedowii*, *T. brizoides* or *T. melvillei*) are clear dominants at most sites. Such species were highly influential in determining floristic gradients and major groupings even following severe (log) transformations. Despite this, the sub-dominant and uncommon tree and shrub species were important in determining communities within the vegetation subtypes.

A major gradient in species composition identified corresponds to the topographic sequence from hill or mountain top to valley floor (i.e. catena) typical of the northern and eastern parts of the study area where the topography consists of a series of well defined ranges and ridges of ironstone formations with intervening broad valley systems. Many of the major species of the study area are associated with this floristic gradient (e.g. *A. aneura*, *T. basedowii*, *E. leucophloia*). A sequence of communities was also recognised along such catenae. A catenary pattern of relatively distinct communities has been described many times for arid, mountainous areas (Wierenga *et al.* 1987; Cornelius *et al.* 1991; Parker 1991; Cowlishaw & Davies 1997) and has been described as a characteristic feature of such regions (Ayyad 1981). The general catenary sequence found in the northern part of the study area can be summarised as follows: i) hummock grassland (HG) with *E. kingsmillii* on mountain tops; ii) HG with *E. leucophloia* (one of three communities depending on substrate and soil) on upland slopes; iii) HG with *E. gamophylla* on pediment slopes; iv) HG with sparse *A. aneura* (mulga) on bajada slopes and outwash areas; v) mulga woodland with tussock and other grasses on alluvial flats. Large drainage basins have an additional community dominated by *E. victrix* and tussock grass below the mulga woodlands, whereas broad drainage lines, where present, have woodland of *E. xerothermica* with tussock grass understorey and major streams have tall woodland dominated by *E. victrix* and *E. camaldulensis*. It is clear from the descriptions given that several communities are strongly associated with particular geomorphological features. There is also evidence of a secondary differentiation (within landforms) by geological substrate; floristically distinct communities were found on uplands of the Marra Mamba Iron formation, Brockman Iron formation and volcanics, for instance. Relationships between vegetation patterns and environmental variables will be further explored in a subsequent paper. Vegetation studies of the greenstone and ironstone ranges of the Eastern Goldfields (Gibson *et al.* 1997; Gibson & Lyons 2001) have demonstrated the importance of soil type in determining plant communities, with much of the edaphic variation linked to catenary patterns in landform and surface geology.

Although several communities are floristically distinct, others appear to be transitional, either in spatial terms (e.g. ecotones or ecoclines) or in temporal terms (different seral or successional stages). Differential profiles enable one to simultaneously characterise the nature of transition zones in both spatial and floristic terms. In this way they have an advantage over ordinations which show patterns based on floristic similarities only. Differential profiles describe beta diversity (i.e. species turnover) along topographic gradients (Whittaker 1965; Whittaker 1972). The differential profile of a typical catena of the study area (Marandoo) shows that some communities are relatively discrete with only a narrow zone of transition with surrounding communities, whilst others clearly intergrade (spatially) with other communities. These two contrasting types of transition have often been described as ecotone and ecoclines respectively (van Leeuwen 1966; van der Maarel 1990). Hypothetically, transition types form a continuum between these two extremes (van der Maarel 1976), although Hobbs (1986) recognised 5 discrete types of transition in the field, each with their own characteristic pattern of species turnover and controlling factors. Narrow ecotones (i.e. particularly rapid spatial transitions between communities) are evident in the landscape as vegetation boundaries. Essentially two types of narrow ecotones have been recognised: *structural boundaries* where more-or-less only the dominant species of the upper stratum change dramatically (e.g. many savanna – forest boundaries) and *floristic boundaries* where there is an overall change in species composition over a short distance (Wiens *et al.* 1985; Hobbs 1986). Selective disturbance has been attributed as a cause of the first type of ecotone (e.g. the elimination of trees in part of the transition zone by disturbance), whereas the second is seen as the response of two distinct and relatively homogeneous environments meeting (van der Maarel 1976; 1990). The differential profile of this study suggests that transitions between HG communities on hill slopes and HG on upper pediments are ecoclines implying a gradual change in controlling environmental factors, although with considerable point to point variation in these factors. Such a pattern would be expected given the gradual change of slope moving from upland to pediment. The *T. melvillei* HG on bajada slopes (community 5) is spatially distinct from communities upslope and downslope. Transitions between these communities can therefore be described as narrow ecotones although each seems to of a different type. The transition with *T. basedowii* HG upslope seems to be more of a floristic boundary as there is a rapid turnover of species, whilst the transition with mulga woodland downslope (community 6B) is likely to be a structural boundary (given little change in species composition apart from the dominant species). Van Leeuwen *et al.* (1995) who studied the mulga woodlands of the study area, also recognised this distinctive *T. melvillei* HG community and postulated it was the result of recent fire within mulga woodland with hummock grass understorey on alluvial slopes. Indeed observations of burnt mulga stems in this community support this hypothesis. Van Leeuwen *et al.* (1995) felt that given sufficient time (without fire), this community would return to a mulga-hummock grass mix such as community 6B. In other words, these two communities (5 & 6B) may be successional stages of the same community. Van Etten (1988) found structural boundaries between mulga woodlands with hummock grass understoreys and hummock grassland elsewhere in the Hamersley Ranges and hypothesised that, on gradual slopes at least, they were the result of differences in fire regimes: hummock grasslands burn on a regular basis, whilst mulga communities rarely burn and contain many fire sensitive species. Mulga itself is a fire sensitive species and, although it has a limited capacity to regenerate from rootstock, it is vulnerable to repeated fires (Fox 1985; Hodgkinson 2001). Fire then is a possible cause of these structural boundaries between communities 5 and 6B. Long-term monitoring of boundaries is occurring in the study area to confirm the dynamic nature of these boundaries (A.N. Start, pers. comm.). The floristic boundary upslope of the *T. melvillei* – mulga communities suggest a distinct environmental change along the gentle pediment and bajada slopes. It is hypothesised that this change corresponds to the change from Tertiary, consolidated, colluvium deposits of the pediments with their typical ironstone pavements to more recent alluvium deposits typical of bajada and alluvial fans. Transitions between communities further downslope could not be identified because of inadequate sampling in the transition zones. Clearly there is a need to sample more intensively along catenae and to replicate studies over a variety of topographical gradients elsewhere in the study area to clarify transition types between communities and to test hypotheses generated here relating to spatial change between communities. The single catena studied here, however, demonstrates the usefulness of transects in describing vegetation patterns in real space, and that transitions between communities identified along the toposequence vary considerably in terms of width and other characteristics. Austin (1989) and Austin & Smith (1989) recommended the study of transition zones as an important adjunct to ordinations and classifications to clarify the spatial features of transitions.

In the south-western portion, geology and landform are considerably more complex compared to the ironstone ranges and intervening broad valleys elsewhere in the study area. Geological formations, which influence surface soils, comprise a range of volcanics (varying from ancient Archaean granites and gneisses to lower Proterozoic basalts to dolerite intrusions of various ages) and calcareous sedimentary deposits (Proterozoic sandstones and dolomites to Tertiary limestone/calcrete). Although three communities were recognised as existing on these substrates, they were relatively heterogeneous. As time and access constraints did not enable the full topographic and geological variation to be adequately sampled, there remains a strong likelihood that more communities can be defined in the southern half of the study area. One possible community is *A. victoriae* – *A. bivenosa* open shrubland (with chenopods) on calcareous flats. Mulga communities with understoreys different from that described here (e.g. dominated by *T. pungens* and *Eremophila fraseri*) are known for volcanic uplands of the area. Greater sampling is recommended for this portion of the Hamersley Ranges. Furthermore, a number of known landform types were not sampled in the study area as they occurred in small patches/narrow bands (and therefore were beyond the scale of the study) or were not encountered. These included scarps and cliff faces, patches of cracking clays, gorges and narrow drainage lines through pediments, all of which contain a fairly discrete suite of species and, frequently, species restricted to those landforms.

The classification presented here therefore should not be regarded as a comprehensive or an ultimate account of plant communities of the Hamersley Ranges. Rather it is a preliminary classification scheme on which to build and modify as more land around the study area is sampled. Further sampling is also needed to confirm those communities which were shown to differ according to classification methodology, or were otherwise poorly sampled and/or relatively heterogeneous. Based on observations made by the author and others, the vegetation subtypes identified seem fairly ubiquitous and consistent across the region, and extension of the classification would most likely come in the form of additional communities within subtypes. A comprehensive, robust classification for the region would be of considerable benefit for those involved in conservation planning, land management and environmental impact assessment, especially if the various plant communities and other vegetation units were accurately mapped to provide information on their spatial extents and patterns (van Etten 1998). Such an extensive study of flora and vegetation will accompany the Pilbara Biological Survey which commenced in mid 2003. It is also argued that the classification methodology used here has advantages over others employed for the region as it is based on floristics (and hence seeks to maximise the variation in species composition among vegetation units), is hierarchical (and so amenable to different scales), and is based on congruence among different approaches. This latter feature would lead toward a more objective and robust classification given the wide variety of choices made in terms of cut levels, data type and transformation, classification algorithm, and the like (Legendre & Legendre 1998).

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Notes on ....

Powdery bark in *Eucalyptus accedens* deters arthropods? An evaluation using ants

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Abstract. Powderbark wandoo (*Eucalyptus accedens*) has a powdery triterpenoid-containing substance on the surface of its smooth bark, which is formed from sloughing peridermal cells. When compared with the similar-appearing wandoo (*E. wandoo*), which occurs in the same area and which does not accumulate powder, fewer bark-associated arthropods are found. Exposure to this powder accelerated mortality of the ant, *Iridomyrmex chasei*, a species that tends scale and other sap-sucking insects on the foliage of eucalypts. Ants of this and two other species were unable to reach baits on the top of vertical wooden dowels that had been coated with powder taken from the bark of *E. accedens*. The powder may deter arthropods from living or moving on the bark by chemical or physical means. It is postulated that the function of the powder is to reduce the threat from herbivorous or scale-tending arthropods that may live on, or traverse, the bark of this species.

Keywords: Tree trunk, invertebrate, *Eucalyptus* forest, powder, *Eucalyptus accedens*.

Introduction

Bark provides a wide range of refugia for invertebrates and represents an important source of nutrition to such animals, either directly, or through the fungi, lichens, algae and microorganisms that live on and within it. It also acts as a resting place for invertebrates that move within or across the area in which the trees occur. As part of a larger study of the fauna associated with trunks of Australian eucalypts, we recently examined the arthropod fauna associated with wandoo (*Eucalyptus wandoo*) and powderbark wandoo (*E. accedens*) in the Western Australian wheatbelt (Majer *et al.* 2002, 2003).

Both species possess exfoliating bark and have smooth, light-coloured trunks that are similar in appearance. Powderbark wandoo differs from wandoo in having a bark that is covered in a powdery substance, from which it receives its name. Majer *et al.* (2002, 2003) quantified the species richness and general abundance of various arthropod orders on the bark of these two tree species. They found that powderbark wandoo, when compared with wandoo, yielded generally lower numbers of arthropods (6301 *vs* 7754 individuals in bark traps on 20 trees) and fewer species (422 species from 140 families *vs* 497 species from 159 families in bark plus intercept traps on 20 trees). These differences were significant for many of the invertebrate orders.

Measurements of nutrient content of live and dead bark of the two tree species indicated some significant differences (Majer *et al.* 2003), but these differences were not consistent across elements, suggesting that nutrient levels are not a major determinant of the trends in arthropod levels on the two tree species. Our observations also indicate that there are no large differences in the bark roughness, presence of fissures, or general heterogeneity of bark microhabitats between the two species (see photos in Majer *et al.* 2002, 2003). It therefore appears that nutrient levels or gross bark texture is not related to the differences in arthropod assemblages between the two tree species.

There are examples in the literature of leaves, fruits or stems of plants being covered with microscopic crystals of epicuticular wax, which may protect the plant against herbivorous invertebrates (Stork 1980; Edwards 1982; Eigenbrode 1996; Juniper 1995) or Hemiptera-tending ants (Haberlandt 1909). In view of the similarity in appearance of the trunks of the two eucalypt species in our study, and also the fact that they grow at the same sites, we postulated that the powder on the bark of powderbark wandoo contributed to the observed differences in arthropod abundance and richness. In this note, we report on the origin and nature of the powder of powderbark wandoo and the possible role of the powder in limiting arthropod use of the trunk of the tree.

Methods

The study was undertaken in wandoo/powderbark woodland at Dryandra (32° 56'S, 117° 11'E), southwest Australia, approximately 160 km south-east of Perth. Trees were distributed throughout a 20 ha section of the administrative compartment known as Peters Block; powderbark wandoo trees tended to be on the upper half, while wandoo trees tended to be on the lower half of the landscape. Except where indicated, all measurements and samples were taken at 1.5 m above the ground. It was not possible to measure live bark because it merged in with other living tissue of the trunk. However, both species decorticate bark, so the thickness of 10 samples of freshly-fallen bark beneath each tree was measured with a micrometer.

Powder was collected from powderbark wandoo trees using a clean paint brush by brushing the trunk in a downwards motion into a plastic food container. This material was stored in a refrigerator at 4°C. Sub-samples were plated on malt agar to see if there were any associated microorganisms. These were identified by a local specialist. A Liebermann-Burchard test (Brieskorn and Herrig 1959) was performed on the powder to test for the presence of triterpenoids. Slivers of phelloderm of both species were also collected for sectioning and microscopic examination.

To examine the impact of powder on arthropods, five filter paper discs were dipped in bark powder, and the surplus was shaken off to leave a film of powder of similar thickness to that on the trunks. These, and five clean filter papers, were individually placed in petri dishes. A drop of water was added to maintain moisture. Five worker ants (*Iridomyrmex chasei*) were then placed in each petri dish and the lids were replaced. Dishes were maintained in darkness at 20°C, with a drop of water added daily, and observed at 12 h intervals to record the numbers of live and dead animals. This experiment was conducted at Curtin University using locally-collected ants. However, *I. chasei* also occurs at Dryandra and is known to ascend the trunks of various tree species, where it tends sap-sucking insects (Hemiptera).

A further experiment was performed in the vicinity of Curtin University in which 20 cm long, 13 mm diameter wooden dowels were lightly dusted with powder from the powderbark wandoo trees and the upper end was coated with dilute honey bait. Ten powdered and 10 powder-free dowels were then 'planted' vertically in the ground and continuously observed over a 24 h period. Ants that climbed the dowels to reach the honey were scored and collected for subsequent identification. This experiment was performed on 5–6 April 2003 and again on 1–2 May 2003; the second experiment differed from the first in that the dowels were placed at an angle of 45° from the vertical in order to make them easier to climb.

Results

Powderbark wandoo had a much thinner exfoliated bark than wandoo (mean ± SD: 0.28 ± 0.20 *vs* 1.16 ± 0.45 mm). Examination of the powderbark wandoo bark surface under a stereo-microscope revealed a coating of peridermal cells that were sloughing off, either in clumps or singly. Examination of the powder that had been brushed from the trunk indicated that this comprised of sloughed-off peridermal cells, with powder grains measuring on average 35 µm in length. The cells appeared to be empty, although some contained structures that may be fungal hyphae. Plating of the sub-sample of powder revealed the presence of a range of common saprophytic, epiphytic fungi (*Scytalidium* sp., *Aspergillus* sp., *Ulocladium* sp., *Aureobasidium* sp.), whose presence would be expected on decaying organic matter. The chemical analysis of the powder confirmed the presence of triterpenoids. Wandoo bark was similar in appearance and also exhibited sloughing peridermal cells, which did not accumulate to form a powder.

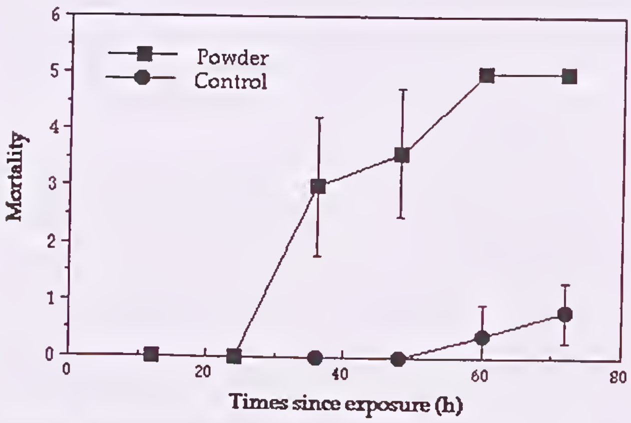

Figure 1. Mean mortality (number of ants per dish ± SD) of *Iridomyrmex chasei* ants (n = 5 replicates of 5 ants per dish) exposed to discs of filter paper that have, or have not, been coated with powder from the bark of powderbark wandoo trees.

Ant mortality was much greater on the powdered paper discs than on the control discs (Fig. 1), with all ants on the powdered discs having died after 72 h, compared with only 1 death per disc in the controls. Inspection of dead ants indicated that the powder had adhered to their body surfaces, with the greatest concentration around the mouthparts and on the tarsi.

All ant species that ascended the dowels were common species that also occurred at Dryandra. In the first baiting experiment, single individuals of *I. chasei*, *Pheidole ampla perthenesis* and *Paratrechina longicornis* ascended the clean dowels to reach the bait; although several ants attempted to climb the powdered dowels, only one ant (*I. chasei*) ascended a powdered dowel, and this ant fell off after climbing half the distance. In the second experiment, in which dowels were set at a 45° angle, ants reached the honey bait on seven of the 10 clean dowels (mean ± SD: 2.5 ± 2.2 ants), but no ants successfully ascended those that had been powdered; all ants were *P. longicornis*.

Discussion

Our findings suggest that the powder of powderbark wandoo trunks may be responsible for the lower usage of trunks by arthropods, when compared with the similar appearing, and co-occurring wandoo tree species.

The powder of powderbark wandoo trunks may influence arthropods in a number of ways. The triterpenoids or other unknown chemicals in the powder may have a repellent or toxicity effect against arthropods. Repellency is a possibility that we did not test directly, although it is noteworthy that the powder was odourless to humans. Our bioassay with *I. chasei* shows that the powder is capable of causing direct insect mortality, which could have been caused by the toxic triterpenoids or other chemicals in the powder. Evidence against this is the fact that ants attempted to climb the dowels, even when powder was present. Toxic or repellent effects of chemicals in the powder could be tested in the future by exhaustive solvent extraction of the powder before conducting boassays.

Secondly, the powder may have blocked the spiracles of certain arthropods, hence interfering with their normal respiration. Close inspection revealed that this did not happen, as the powder grains are at least double the diameter of the spiracles of *I. chasei*, which are of a size that is typical of many bark-associated arthropods.

Thirdly, the powder may render the bark difficult to walk on. This is supported by the concentrations of powder that had accumulated on the tarsi of ants which were exposed to this material, and also the fact that few or no ants were able to climb the powdered dowels. A similar mechanism has been reported in the pitcher plant, *Sarracenia purpurea*, in which wax inside the pitcher sloughs off when insects attempt to climb out, causing them to fall into the fluid within (Juniper 1986). Wax blooms on the stems of various species of *Macaranga* have also been found to prevent ants from walking across them (Federle *et al.* 1997), and wax layers on the surface of juvenile *Eucalyptus nitens* and *E. globulus* prevent chrysomelid beetles from adhering to their surface (Edwards 1982).

The final possibility is that the powder is simply a physical nuisance to the normal movement and activity of animals to which it adheres. The accumulation of powder around the mouthparts of the *I. chasei* we studied suggests that they tried to remove the powder from their bodies. Possibly this diverted their attention or energy for climbing the trunks of *E. accedens*. Whatever the explanation, our bioassay with dowels shows that the powder effectively prevents ants from climbing the dowels, and thus can deter ants and potentially other arthropods from climbing the trunks.

There may, of course, be other reasons why this tree species accumulates powder on the surface of its bark. Our data in Majer *et al.* (2002) indicate that the invertebrates that are apparently deterred from walking on the powderbark wandoo trunks represent several feeding guilds. Importantly, ants and sap-sucking hemipterans are noticeably less diverse on the powderbark wandoo than the wandoo (43 *vs* 54, and 9 *vs* 15 species respectively in bark traps) (Majer *et al.* 2002). The powder does not totally exclude trunk-associated arthropods but, by reducing the abundance of bark-feeding species on the trunk, and by making it more difficult for folivores to reach the canopy of the tree (Proctor *et al.* 2002), the powder on the bark of *E. accedens* may reduce the overall levels of herbivory and associated injury to the tree.

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Reptile assemblage of the Abydos Plain, north-eastern Pilbara, Western Australia

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Abstract

A seventy-four day survey extending over three years recorded a diverse herpetofaunal assemblage of 72 species. Five frog species were recorded after episodic rainfall events, while fifteen snake species and one turtle were infrequently recorded. Data from 51 lizard species showed strong habitat preferences. Lizard assemblages on loams associated with creek lines differed from those on the sands of the Abydos Plain and those adjacent to rocky substrates. These habitat preferences, marked seasonal patterns in activity, and a high proportion of rarely captured species indicate that additional species probably remain to be recorded. Fire had a marked effect on the abundance and composition of species in *Triodia* habitats on sandy soils with burrowing and fossorial forms surviving best.

Keywords: herpetofauna, lizards, diversity, variation, habitat preference, fire response

Introduction

The diverse herpetofauna of Australia's arid regions came to international prominence with the pioneering work by Pianka (1969, 1986) and Pianka & Pianka (1976) and the comparisons that were made between lizard assemblages in desert regions of North America, Africa and Australia. Those studies have now been extended for over thirty years (Pianka 1996) and have made a major contribution to the field of community ecology as well as our understanding of lizard assemblages in arid Australia.

The arid zone of Australia covers over 55% of the continent (Williams & Calaby 1985), but studies of arid zone reptile species have mainly focussed on populations and assemblages in *Triodia*-dominated habitats of central Australia (James 1994; Downey & Dickman 1993; Masters 1996) and the Great Victorian Desert (Pianka 1986, 1996) with some studies in more heterogeneous areas of the southern arid interior (Read 1995; Smith *et al.* 1997; Thompson *et al.* 2003a; Cowan & How 2004). There have been no published studies examining the herpetofauna of the extensive arid Pilbara region of Western Australia.

The Pilbara bioregion covers 179 287 km^2 (Thackway & Cresswell 1995) and is considered to comprise four subregions (McKenzie *et al.* 2000). One of these, the Chichester subregion, consists of Archaean granite and basaltic plains covered by shrub steppe of *Acacia pyrifolia* and *Triodia pungens* with Snappy Gum (*Eucalyptus leucophloia*) tree steppes on the ranges. This component encompasses the Abydos Plain, the major landform on Woodstock and Abydos stations of the northeastern Pilbara (Tinley 1991a).

Despite the large area and extensive anthropogenic activity in the Pilbara, there have been few attempts to document the faunal diversity of the region on a systematic basis (Dunlop & Sawle 1980; R.Teale, Biota Environmental Sciences unpubl; P.K Kendrick, CALM Karratha unpubl.) The herpetofauna of the Pilbara is known to have high endemism with many species confined to small geographic areas within the broader limits of the Pilbara bioregion (Storr *et al.* 1983, 1990, 1999, 2002).

As part of a three year survey to document the faunal diversity of Woodstock and Abydos stations, data were gathered on the composition and structure of numerous vertebrate assemblages in the area (How *et al.* 1991; How & Cooper 2002) to provide baseline information on species habitat preferences and diversity for future management of the area (Berry *et al.* 1991). Woodstock and Abydos stations cover an area of over 150 000 ha of the north-eastern Pilbara and have been the focus of several pioneering biological studies of the arid zone in Western Australia including plants (Burbidge 1943, 1945, 1959), mammals (Ealey 1967a, 1967b, 1967c) and fire (Suijendorp 1967).

In this study, we examine the composition and habitat relationships of the reptile assemblages on the extensive Abydos Plain over a three-year period and compare this information with other studies of reptile assemblages in arid Australia.

Survey Methods

Woodstock and Abydos stations lie some 150 km south of the township of Port Hedland, and the study area covers the upper reaches of the Yule and Turner Rivers that drain northwesterly across a major physiographic unit of the Pilbara, the Abydos Plain. Over the three years of this study, rainfall showed appreciable seasonal and annual variation (Table 1). Major episodic rainfall events in March 1988, during the first survey period, and February 1989, after the fourth survey, flooded Coorong Creek and all other ephemeral streams and drainage lines associated with it.

Table 1

Rainfall registered at Woodstock Station for each month between January 1987 and October 1990 and the mean for 1905 to 1989. Data from the Bureau of Meteorology WA.

Years	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	TOTAL
1987	95.2	78.8	–	–	4.8	–	8.5	–	–	–	–	23.0	210.3
1988	61.9	10.0	252.2	8.0	109.2	0.8	–	49.7	–	0.4	1.9	72.4	566.5
1989	63.4	227.0	0.4	46.2	9.0	117.9	2.3	–	–	–	4.0	11.2	484.4
1990	79.2	6.6	–	–	–	3.4	–	–	–	–			
Mean 1905-89	77.5	64.7	59.0	21.1	22.5	25.2	9.9	5.8	1.5	3.1	8.3	36.2	334.8

Sampling Sites and Climate

The regional landforms and vegetation of the Abydos/Woodstock area were described in detail by Tinley (1991b) and formed the basis of selection of sampling sites for the study of small vertebrates (see Fig 5.1, How *et al.* 1991).

Eight major sampling sites, representing the principal habitats identified on the sands of the Abydos Plain, were selected for intensive pit and cage trapping programs and opportunistic collecting. An additional 20 subsidiary sites were selected to sample the granite tors on the Abydos Plain and adjacent rocky escarpments of the Gorge Fold Ranges where substrates precluded the use of pitfall traps.

The eight major sampling sites were:

WS1 *Eucalyptus camaldulensis, Melaleuca leucadendra* 5-8 m tall, 35% canopy cover, over *Acacia* sp. 1-2 m tall, *c.* 5% canopy cover over *Cenchrus ciliaris* <0.5 m tall, *c.* 90% canopy cover. Deep alluvium supporting a narrow belt of riverine woodland on the edge of Coorong Creek. 21°37′01″S, 118 ° 57′13″E

WS2 *Acacia pyrifolia*, 2–3 m tall, 3% canopy cover, *Hakea suberea*, 2–3 m tall, <0.5% canopy cover and *Acacia* sp. 2–3 m tall, <0.5% canopy cover over *Triodia* spp. (2) *c.* 0.5 m tall, 80% canopy cover. Coarse sandy loam with granite bedrock at 30–40 cm and located 200 m from Coorong Creek. Site was burnt in January 1990. 21 ° 36′42″S, 118 ° 57′20″E

WS3 *Triodia* spp. <1 m tall *c.* 60% canopy cover with occasional *Acacia* spp. as emergents. Red sandy loam in an ephemeral drainage line. Site was burnt in January 1990. 21 ° 36′35″S, 118 ° 57′44″E

WS4 *Acacia pyrifolia*, 2–4 m tall, *c.* 5% canopy cover, over *Acacia ancistrocarpa*, 1.5–2 m tall, 50%–70% *Triodia* spp. canopy cover. Occasional ephemerals after rain. Red sandy loam soil, >60 cm deep. Site was burnt in January 1990. 21 ° 36′34″S, 118 ° 58′28″E

WS5 *Triodia secunda* and *T. longiceps* <0.5 m tall, *c.* 70% canopy cover. Soil was white sandy silt over clay. 21 ° 36′35″S, 118 ° 59′16″E

WS6 *Acacia orthocarpa*, 3–4 m tall, *c.* 7% canopy cover, and occasional *A. pyrifolia*, over *Triodia lanigera c.* 0.5 m tall, 50% canopy cover. Skeletal red granitic sandy soil. 21 ° 36′35″S, 119 ° 01′17″E

WS8 *Eucalyptus terminalis*, 3–5 m tall, *c.* 2% canopy cover, over oval leaf wattle 1–1.5 m tall, *c.* 2% canopy cover, over *Triodia c.* 0.5 m tall, *c.* 40% canopy cover. Site includes valley between, and the steep slopes of calcrete mesas. Valley soil is calcareous clay loam. 21 ° 36′25″S, 119 ° 02′23″E

WS10 *Acacia* sp. 1.5–2.5 m tall, <0.5% canopy cover, *Hakea* sp. 1.5–2.5 m tall, <0.5% canopy cover, over *Acacia* sp. <1m tall, *c.* 3% canopy cover, over *Triodia* sp. <0.5 m tall *c.* 60% canopy cover. Deep red loamy sand. Extensive surface water after heavy rain. 21 ° 40′15″S, 119 ° 02′30″E

Fires were frequently seen around the study area during the dry summer months, and numerous small areas on the eastern edge of Woodstock Station were burnt in January and February 1989. In January 1990, lightning strikes started several small fires; three of which burnt out sampling sites WS2, WS3 and WS4 and parts of the surrounding areas. The remaining major sampling sites showed no evidence of having been burnt for numerous years.

Sampling Methods

At each of the eight major sampling sites, a line of fenced pitfall traps that comprised a 50-m long by 30-cm high fly screen mesh fence that crossed six pitfall traps inserted 600 mm into the substrate was established. Pitfall traps were generally made of 175 mm diameter PVC pipe 600 mm deep, but at several sites where the soil was less than this depth, the piping was replaced by 400 mm deep conical pits. At each of the eight major sampling sites, a line of 15 Elliott Type A traps, baited with universal bait, were set 15 m apart and within 50 m of the fenced pitfall trapline. Traps were checked twice daily, shortly after dawn and again in the late afternoon.

At most of the 20 subsidiary sampling sites only Elliott Type A traps were used but on some rockpiles the larger Type B Elliott traps were interspersed with the smaller traps.

Sampling was undertaken between 21–31 March 1988, 2–9 May 1988, 22–30 September 1988, 9–17 February 1989, 16–24 April 1989, 16–24 September 1989, 26 February–7 March 1990, 25 July–2 August 1990 and 24 October–1 November 1990. Sampling was designed to cover summer (February–March) and spring (September–October) in each of the three years, with three additional sampling periods to examine activity at other times of the year. Routine trapping of the 8 major sampling sites and the 20 subsidiary sites was undertaken on all surveys except for May 1988, when only the fenced pitfall traplines were operated, and April 1989, when only Elliott traplines, in the subsidiary sampling sites, were set. All major sampling sites were also subjected to daily routine searching methods and nocturnal head-torching to document herpetofauna not prone to capture in the

Elliott or pitfall traps. Subsidiary sites were checked daily for captures in Elliott traps, but also searched opportunistically (using a head-torch for night searches).

Pitfall traplines were operated on 61 days of the 72 days over which sampling occurred.

All individuals captured were identified, measured and weighed prior to release. For several lizard taxa, individuals were also marked by toe-clipping before release. Voucher specimens were taken of all lizard species and examined in the laboratory to determine their sex and reproductive condition and to collect tissue samples for later molecular studies. The stomach contents of voucher specimens have been published separately as a study on the diet of selected species (Twigg *et al.* 1996).

Analyses

Assemblage analyses were carried out using the NTSYS (2000) program with an examination of the Bray-Curtis index of dissimilarity matrix clustered using the UPGMA method.

Measures of diversity and evenness were derived from the software package on ecological methods (Krebs 2000) using the Shannon measure [H] and the α of the log series for diversity assessment and the Simpson index [E] for evenness.

Results

Herpetofaunal Assemblage

The known herpetofaunal assemblage of the Abydos/Woodstock stations consists of 5 species of amphibians in two families, 15 species of snakes in three families, a turtle and 51 species of lizards from five families (Table 2).

The only species previously known to occur on the study area but not collected during this survey were a legless lizard, *Delma nasuta*, and a skink, *Ctenotus schomburgkii* (Table 2). Both of these species were collected in the late 1950's, and an additional specimen of *Delma nasuta* was collected in 1963 (WA Museum records).

During the final survey in October 1990, the second records of each of the elapid snakes *Acanthophis wellsi* and *Pseudonaja modesta* were obtained; single specimens of these had previously been collected in 1959 and 1958 respectively (WA Museum records). However, Chapman (WA Museum pers. comm.) had seen *A. wellsi* in 1981 near the airstrip and K. Young (WA Museum pers. comm.) recorded this species at Woodstock Homestead indicating that the species may be widespread but not commonly recorded. The only previous specimen of the blind snake *Ramphotyphlops grypus* from Woodstock was collected in 1953 (WA Museum records). The addition of 25 previously unrecorded species during this survey of Abydos/Woodstock and the continued increase of new species recorded during the 72 days of sampling over three years suggests that additional species of reptile could still be recorded from the area (Fig 1).

Activity of herpetofaunal species is strongly seasonal (Table 3) . The highest number of species and individuals were recorded in the summer sampling period of each year. Fewer species and individuals were trapped during the spring sampling, and far fewer individuals were

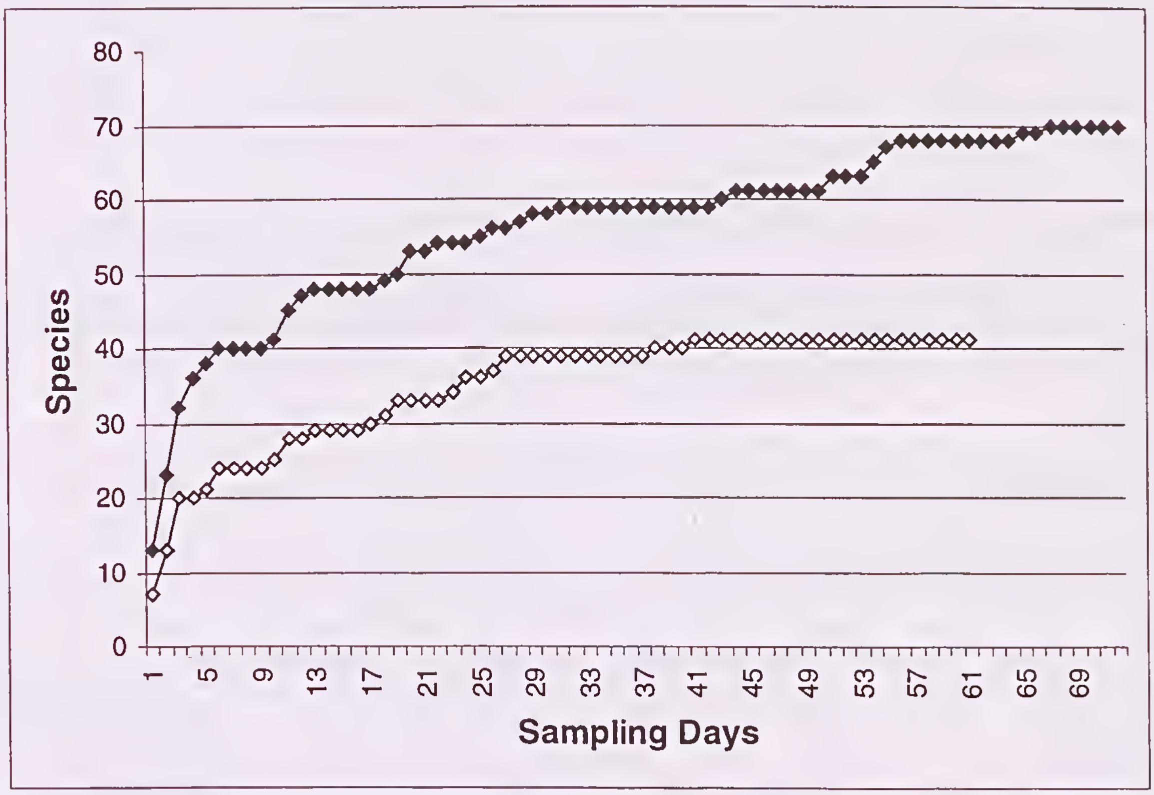

Figure 1. Accumulated capture of herpetofaunal species on the Abydos Plain between March 1988 and October 1990. Solid diamonds represent species captured by all techniques on all sampling days, open diamonds are species captured only by pitfall trapping.

Table 2

The herpetofauna of the Abydos/Woodstock Study area indicating the number of individuals of each species captured at each of the major sampling sites and from all other locations combined. An asterisk [*] indicates the species had been previously collected, and a plus [+] indicates an observational record.

Sites	**WS1**	**WS2**	**WS3**	**WS4**	**WS5**	**WS6**	**WS8**	**WS10**	**Others**
No. pittrap days	288	276	330	348	330	318	318	276	
No. Elliotts	595	605	675	725	675	635	635	485	3101
Hylidae									
* *Cyclorana maini*	39	10	1	1	3	2	3	2	12
* *Litoria rubella*	11	–	–	–	–	–	3	–	34
Myobatrachidae									
* *Limnodynastes spenceri*	82	3	1	2	3	4	–	–	8
Uperoleia glandulosa	2	–	–	–	–	–	–	–	1
* *U. russelli*	81	12	6	–	–	–	4	1	20
Cheluidae									
* *Chelodina steindachneri*	+	–	–	–	–	–	–	–	+
Agamidae									
* *Ctenophorus caudicinctus*	–	1	–	–	–	–	5	2	19
* *C. isolepis isolepis*	–	2	3	9	6	8	–	10	9
* *C. nuchalis*	–	4	8	4	5	–	1	1	6
Diporiphora winneckei	–	–	–	1	–	–	–	1	1
* *Lophognathus longirostris*	4	1	–	–	1	–	2	–	4
Pogona minor	–	1	–	3	1	–	–	2	2
Gekkonidae									
Diplodactylus conspicillatus	–	4	3	9	3	7	–	1	–
D. stenodactylus	1	6	2	6	1	3	3	2	–
Gehyra pilbara	1	2	–	–	–	–	–	–	64
* *G. punctata*	–	–	–	–	–	–	3	–	55
* *G. variegata*	4	–	–	7	–	–	2	–	10
Heteronotia binoei	6	1	1	1	–	–	4	1	1
Heteronotia spelea	–	–	–	–	–	–	–	–	1
* *Nephrurus levis pilbarensis*	1	–	6	2	3	–	–	6	2
Rhynchoedura ornata	–	1	1	4	–	–	4	1	1
* *Strophurus elderi*	–	–	1	1	–	1	2	1	–
Strophurus jeanae	–	1	–	–	–	–	–	–	–
Pygopodidae									
* *Delma nasuta*	–	–	–	–	–	–	–	–	–
* *D. pax*	1	–	–	–	–	1	2	–	1
D. tincta	–	–	1	–	–	–	–	–	–
* *Lialis burtonis*	2	1	2	2	–	–	4	–	1
Scincidae									
Carlia munda	8	–	–	–	–	–	–	–	1
Cryptoblepharus plagiocephalus	–	–	–	–	–	–	–	–	9
Ctenotus duricola	–	1	2	4	10	5	–	6	–
* *C. grandis*	1	61	48	37	31	5	45	14	20
C. helenae	1	9	6	4	2	13	5	7	3
C. nigrilineatus	–	–	–	–	–	–	–	–	2
* *C. pantherinus*	1	1	2	11	7	8	–	19	1
* *C. saxatilis*	7	3	–	–	–	2	27	1	51
* *C. schomburgkii*	–	–	–	–	–	–	–	–	–
C. serventyi	–	–	–	3	–	–	–	2	–
* *Cyclodomorphus melanops*	1	–	–	–	–	–	–	–	–
Egernia depressa	–	–	–	–	–	–	–	–	1
* *E. formosa*	–	–	–	-	-	-	-	-	11
* *E. striata*	-	-	3	7	6	6	-	5	-
* *Eremiascincus richardsonii*	-	-	-	-	-	-	-	-	1
* *Lerista bipes*	16	1	11	5	10	7	-	-	1
* *L. muelleri*	6	1	-	-	-	-	3	-	1
Menetia greyii	1	-	-	-	-	2	-	2	-
* *Morethia ruficauda*	-	-	2	2	-	-	-	-	-
Notoscincus ornatus	1	-	-	-	-	-	-	-	1
* *Proablepharus reginae*	-	-	-	-	-	1	3	-	-
* *Tiliqua multifasciata*	-	-	5	5	2	4	1	4	1

Table 2 (cont.)

Sites	WS1	WS2	WS3	WS4	WS5	WS6	WS8	WS10	Others
No. pittrap days	288	276	330	348	330	318	318	276	
No. Elliotts	595	605	675	725	675	635	635	485	3101
Varanidae									
* *Varanus acanthurus*	1	1	1	2	-	1	4	1	12
* *V. brevicauda*	-	2	-	-	4	2	-	9	-
V. eremius	-	-	1	1	1	-	-	-	1
* *V. giganteus*	-	+	-	-	-	-	-	+	1
* *V. gouldii*	-	+	1	3	1	-	1	+	1
V. panoptes	+	-	-	-	-	-	-	-	-
* *V. pilbarensis*	-	-	-	-	-	-	-	-	2
* *V. tristis*	-	-	-	-	-	-	-	-	3
Typhlopidae									
Ramphotyphlops ammodytes	1	-	3	-	-	-	1	-	-
* *R. grypus*	-	-	-	-	2	-	-	-	-
* *R. pilbarensis*	-	2	-	-	-	-	-	-	-
Boidae									
* *Antaresia perthensis*	-	-	-	-	-	-	-	-	1
* *Antaresia stimsoni*	-	-	1	-	-	-	-	-	3
Aspidites melanocephalus	-	-	-	-	-	-	-	1	-
* *Liasis olivaceus barroni*	-	-	-	-	-	-	-	-	1
Elapidae									
* *Acanthophis wellsi*	-	-	-	-	-	-	-	+	1
Brachyurophis approximans	-	1	-	-	-	-	-	-	-
* *Demansia psammophis cupreiceps*	-	-	-	-	-	-	-		3
* *Furina ornata*	-	-	-	-	-	-	-	-	1
* *Pseudechis australis*	-	+	-	-	-	-	1	1	4
* *Pseudonaja modesta*	-	-	1	-	-	-	-	-	-
* *P. nuchalis*	-	1	-	-	1	-	-	-	2
* *Suta punctata*	-	-	-	-	-	-	-	-	-
Amphibians – Species/Individuals	5/215	3/25	3/8	2/3	2/6	2/6	3/10	2/3	5/75
Turtles – Species/Individuals	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	1/0
Lizards – Species/Individuals	20/64	23/105	21/110	24/133	17/94	17/76	19/121	24/98	35/302
Snakes – Species/Individuals	1/1	4/4	3/5	0/0	2/2	0/0	2/2	3/2	8/16
Herpetofauna – Species/Individuals	27/280	30/134	27/123	26/136	21/102	19/82	24/133	29/103	49/393
Shannon diversity [H]	3.61	2.70	3.17	3.89	3.32	3.71	3.14	3.88	
α log series diversity	9.87	8.99	7.70	8.55	6.06	6.80	6.33	10.01	
Simpson evenness [E]	0.43	0.13	0.22	0.38	0.38	0.22	0.17	0.17	

captured during the three other sampling periods (*viz* May 1988, April 1989, July 1990).

Snakes from the three families were infrequently captured (or recorded) on the major sampling sites, and only occasionally at the 20 subsidiary sites. Consequently, they were not included in the assessment of reptile assemblages in habitats of the Abydos Plain. This also was the case for larger goannas such as *Varanus giganteus*, *V. gouldii* and *V. panoptes* and, although juveniles of these were occasionally pit trapped, these species were also omitted from the assemblage analysis. Most species of snakes in the area were active

Table 3

Number of individuals of each species recorded in the nine sampling periods undertaken at the Woodstock study area between 1988-1990.

Sampling Periods	Mar-88	May-88	Sep-88	Feb-89	Apr-89	Sep-89	Mar-90	Jul-90	Oct-90
No. pittrap days	324	282	312	318	24	240	432	216	336
No. Elliotts	1560	0	1240	900	448	1017	1167	782	1017
Amphibian – Individuals	77	95	14	132	1	14	4	3	1
Amphibians – Species	4	4	3	4	1	2	1	1	1
Lizards – Individuals	187	56	131	215	32	120	248	30	91
Lizards – Species	31	24	32	32	13	25	38	10	25
Snakes – Individuals	6	2	4	4	1	2	11	1	3
Snakes – Species	5	2	4	3	1	2	9	1	3
Reptile α diversity	13.04	18.11	16.06	11.75	9.18	10.72	16.77	6.09	13.49

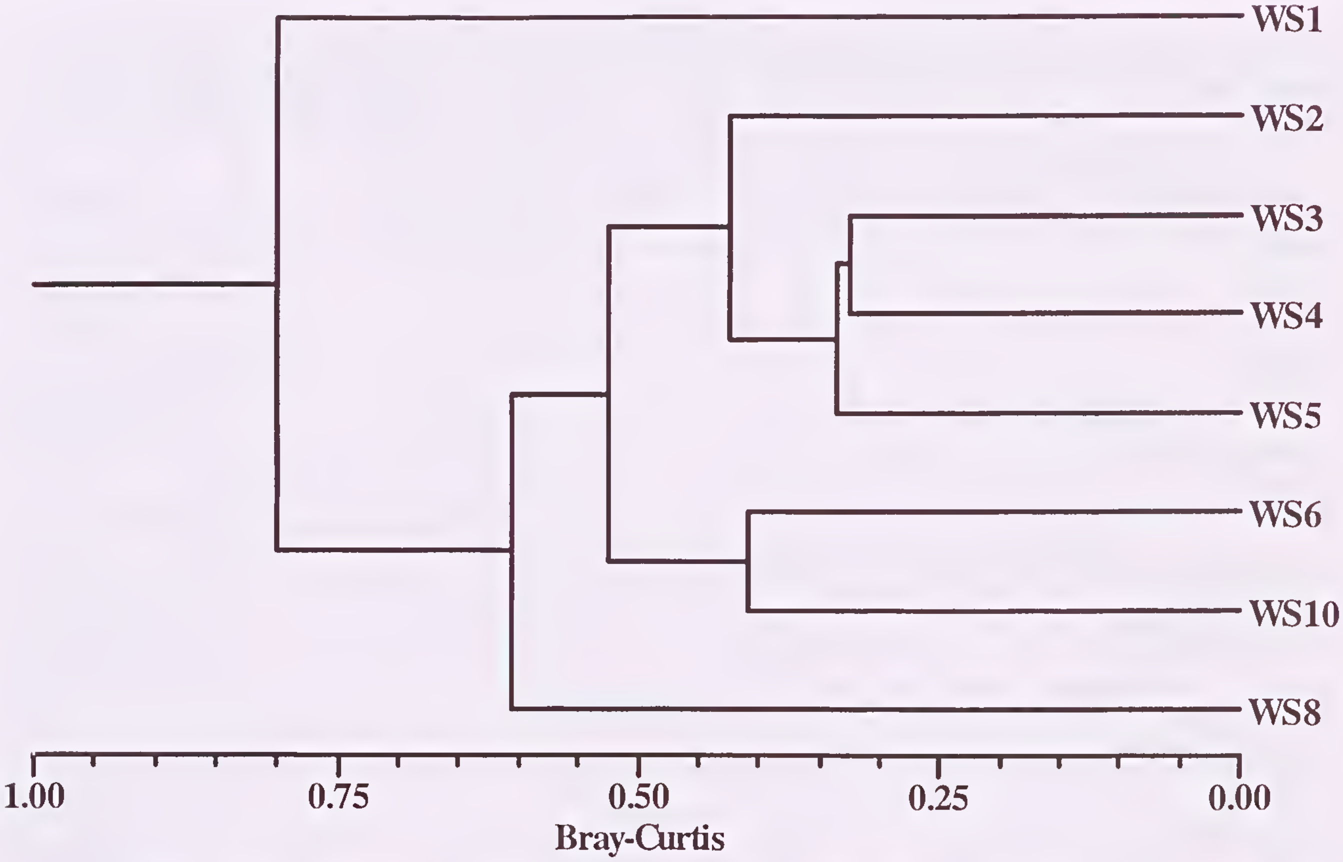

Figure 2. Similarity of lizard assemblages for the eight major sampling sites on the Abydos Plain during the period March 1988 to October 1990.

nocturnally, although *Pseudonaja* spp. and *Demansia psammophis* were seen during the day and *Aspidites melanocephalus* was seen shortly after sunrise.

Amphibians were only captured after summer rain and were most abundant in sites near permanent watercourses, like WS1, and seasonal drainage lines, like WS2. Frogs were also excluded from assessment of assemblages in the major sampling sites of the study area (Fig 2).

Habitat Associations

Although 72 species of herpetofauna are known from the Abydos/Woodstock area, variation was apparent in the number of species caught in the eight major sampling sites with the number of species ranging from 19 to 30 (Table 2).

An analysis of the lizard assemblages from the eight major sampling sites, using the Bray-Curtis index of dissimilarity on abundance data from Table 2 showed that marked differences occurred between habitats (Fig 2). The deeper loams and litter associated with the fringing woodlands of Coorong Creek (WS1) has a distinctive lizard assemblage, as did the habitat adjacent to a rocky breakaway (WS8). The six remaining habitats sampled on the deeper sands of the Abydos plain had assemblages that had similarity of 50% or greater.

Eight lizard species were captured only on subsidiary sites, however, the majority of the 41 lizard species captured on the major sampling sites were also captured on subsidiary sites and these captures provide important complementary assessments of habitat preferences in certain species. Lizards that showed strong preference for rocky habitats and were infrequently captured on sandy substrates included *Ctenophorus caudicinctus, Gehyra punctata, G. pilbara, Heteronotia spelea, Cryptoblepharus plagiocephalus, Ctenotus saxatilis, Egernia formosa, E. depressa, Varanus acanthurus* and *V. pilbarensis.* Species that were generally captured on the extensive sandy loams included *Ctenophorus isolepis, Diplodactylus conspicillatus, D. stenodactylus, Nephrurus levis, Rhynchoedura ornata, Lialis burtonis, Ctenotus duricola, C. grandis, C. helenae, C. pantherinus, C. serventyi, Egernia striata, Lerista bipes, Morethia ruficauda, Varanus brevicauda* and *V. eremius.* Smaller litter-frequenting lizards such as *Heteronotia binoei, Carlia munda, Lerista muelleri, Menetia greyii* and *Proablepharus reginae* were captured where litter accumulated in depth adjacent to watercourses or under larger shrubs. The arboreal species *Lophognathus longirostris, Pogona minor, Gehyra variegata* and *Varanus tristis* were caught at sites where shrubs or short trees predominated.

Effects of Fire on Lizards

Fire initiated by lightning strikes burnt three of the major sampling sites during January 1990. This occurred two years after the survey commenced and the effects of the fire were followed through for nine months over three sampling periods afterwards (Table 4).

The capture of lizard species and individuals from the three major sites that were burnt (WS2, WS3, WS4) and three relatively similar [*c.* 50% similar, Fig 2] sites that

Table 4

Number of pit-trap days at sampling sites burnt in January 1990 (WS 2, 3, 4) and those that remained unburnt throughout the study (WS 5, 6, 10). Species and individuals caught during the two years sampling pre-burn [1988, 1989] and year post-burn [1990] are presented.

		Burnt sites			Unburnt sites	
	88B	89B	90B	88U	89U	90U
SPECIES Pitdays	372	222	360	312	216	396
Diplodactylus conspicillatus	2	3	8	2	3	6
Diplodactylus stenodactylus	3	2	5	2	3	0
Gehyra variegata	0	4	0	0	0	0
Heteronotia binoei	2	1	0	0	0	1
Nephrurus levis	3	3	0	2	2	3
Rhynchoedura ornata	2	0	1	1	0	0
Strophurus elderi	0	1	1	1	0	1
Delma pax	0	0	0	0	0	1
Lialis burtonis	0	4	0	0	0	0
Ctenophorus caudicinctus	0	1	0	0	0	0
Ctenophorus nuchalis	0	1	11	2	1	0
Ctenophorus isolepis	3	1	0	5	8	5
Pogona minor	0	3	0	1	1	0
Ctenotus duricola	2	4	0	6	5	10
Ctenotus grandis	10	8	0	3	2	4
Ctenotus helenae	0	3	0	4	0	4
Ctenotus pantherinus	5	7	0	11	6	12
Ctenotus serventyi	1	1	1	0	2	0
Egernia striata	4	0	5	3	5	8
Lerista bipes	6	2	2	11	4	1
Menetia greyii	0	0	0	1	0	3
Morethia ruficauda	2	0	0	0	0	0
Notoscincus ornatus	0	0	0	0	0	1
Proablepharus reginae	0	0	0	0	0	2
Tiliqua multifasciata	2	0	2	0	0	0
Varanus acanthurus	0	1	0	0	0	0
Varanus brevicauda	2	0	0	4	3	6
Varanus eremius	2	0	0	0	0	1
Varanus gouldii	0	1	1	0	0	0
No. species	16	19	10	16	13	17
No. individuals	51	51	37	59	45	69
Indiv/10 pitdays	1.37	2.29	1.03	1.89	2.08	3.64
Shannon Diversity [H]	3.74	3.90	2.80	3.57	3.47	3.64
Log series diversity [α]	8.00	10.98	4.50	7.22	6.12	7.20
Simpson Evenness [E]	0.69	0.64	0.55	0.58	0.75	0.60

remained unburnt (WS5, WS6, WS10) throughout are presented for each year of sampling in Table 4.

On the burnt sites both the number of species and individuals declined in the nine months post fire and these areas had both a lowered species diversity and evenness (Table 4). In the sites that remained unburnt, species number fluctuated less and both species diversity and evenness showed smaller changes. The similarity of lizard assemblages on the area burnt (B) in the third year and assemblages on the unburnt (U) area over each of the three years is presented in Figure 3. The least similar assemblage was recorded in the area burnt by the fire of January 1990.

The species least affected by fire, at least in the short term, were those that live in burrows or are primarily fossorial. In the burnt sample sites, 32 of the 37 individuals trapped after the fire belonged to the species *Ctenophorus nuchalis, Diplodactylus conspicillatus, D. stenodactylus, Rhynchoedura ornata, Egernia striata* (four of these are nocturnal and all live in burrows) or *Lerista bipes* (which is fossorial).

Discussion

The opportunistic collections of the fauna made over the past 50 years from the 1,500 km² Abydos/Woodstock area has resulted in a substantial body of knowledge on mammals (How & Cooper 2002) and birds (Storr 1984; How *et al.* 1991) but the herpetofauna remains the least known group of vertebrates. The 24 species of reptile and one frog that were recorded on the study area for the first time during this survey included the endemic skink, *Ctenotus nigrilineatus*, which was subsequently described from two specimens collected from one localised rockpile in the study area (Storr 1990).

The herpetofaunal assemblage of the Abydos/ Woodstock area, comprising 5 amphibians and 67 reptiles, is one of the richest recorded in Australia. In a recent review of studies defining the diversity of reptiles in arid and mesic habitats of Australia, Thompson *et al.* (2003a) compared the findings of 14 areas that sampled reptiles at three broad geographic scales, *viz.* bioregional, landscape and biotope. The number of reptile species recorded in the 12 landscape level surveys reported in

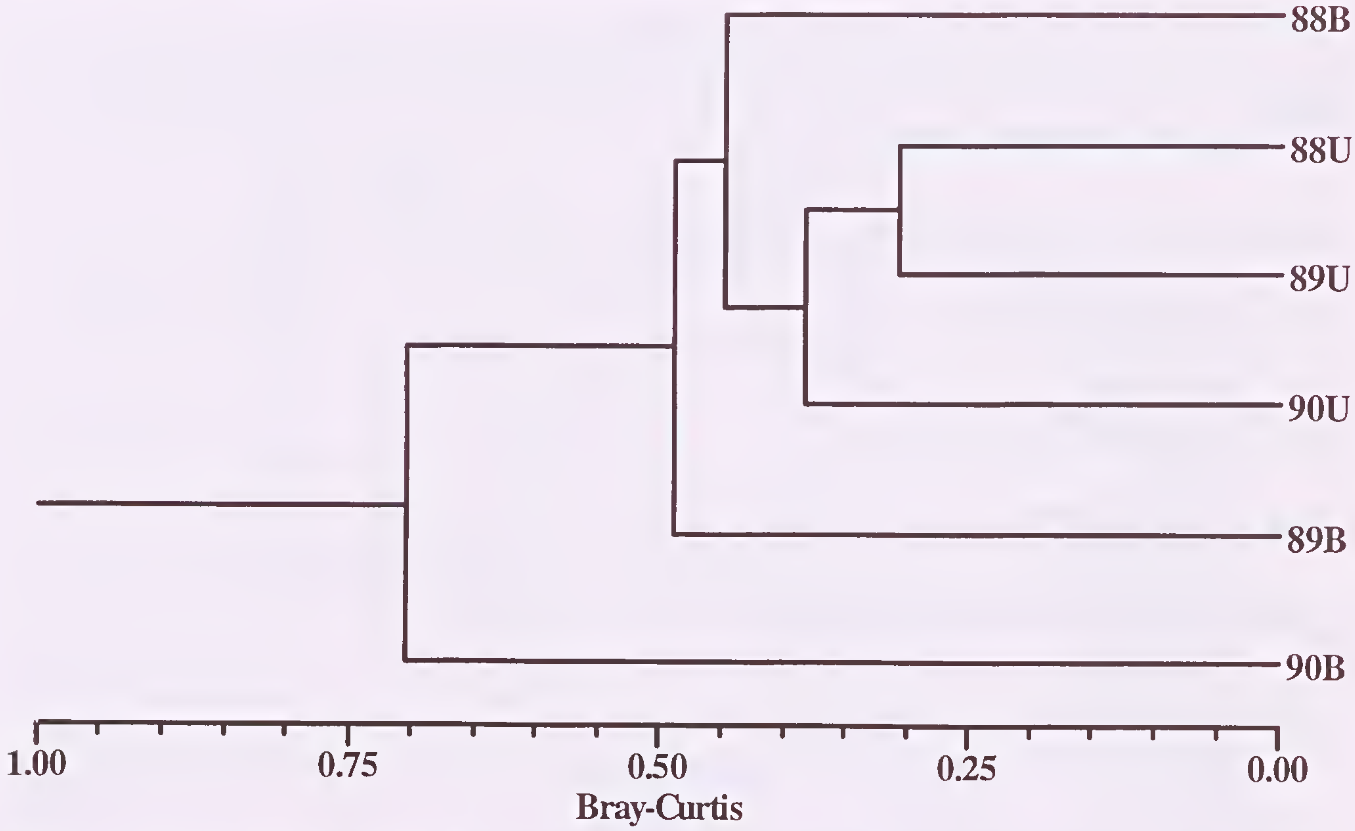

Figure 3. Similarity of lizard assemblages for the three years of study on an area that was burnt (B) by the fires of January 1990 and a similar adjacent area that remained unburnt (U).

the literature, identified between 26 and 68 species, while the two bioregional surveys had 57 and 76 species. The 67 reptiles species recorded at Abydos/Woodstock is, therefore, surpassed only in number by one bioregional survey, the Carnarvon Basin survey by Rolfe and McKenzie (2000) and the Red Sands survey in the Great Victoria Desert of Pianka (1996). The Carnarvon Basin bioregional survey encompassed an area of nearly 92,000 km^2, over 60 times greater than that of the present survey area. However, in contradistinction, the Red Sands survey in the Great Victoria Desert of Pianka (1996) covered around 1 km^2 of *Triodia* dominated red dune landform, indicating that diversity at a small landscape level may also be exceedingly rich in arid desert environments. Thompson *et al.* (2003a) also calculated the Shannon diversity index of their fourteen sites as ranging from 2.00 [Tanami Desert B] to 3.60 [Carnarvon Basin] and the α log series diversity as ranging from 4.05 [Bold Park] to 17.29 [Carnarvon Basin]. The same diversity measures applied to the reptile survey for Abydos/Woodstock area are 4.64 and 14.94, respectively, indicating the exceptionally high diversity of the study area. The total herpetofauna of Abydos/Woodstock is comparable in number (72) to the four times larger Hamersley Range [Karajini] National Park (Johnstone 1983) that lies 200 km to the south.

The Chichester subregion of the Pilbara bioregion contains 105 reptile and 10 frog species in an area that encompasses over 90, 000 km^2 (How & Cowan unpubl.). The Abydos/Woodstock area lies within the Chichester subregion and the 67 species recorded represents 64% of the total known subregional reptile fauna. The five amphibian species recorded in this survey represent only 50% of the total amphibian fauna documented for the subregion.

Snakes generally are infrequently captured or observed during herpetofaunal surveys (How 1998; M. Cowan, CALM Kalgoorlie pers. comm.) such that their true representation in reptile assemblages is often underestimated by short-term sampling surveys. This is clearly demonstrated in the data compiled in Thompson *et al.* (2003a), where snakes reach their highest proportion in assemblages in studies that have the longest temporal span, *e.g.* Bold Park (How 1998), Red Sands (Pianka 1996) and Bungalbin (Withers unpublished). During the present study each of the 15 species of snakes contributed less than 0.5% of individual records, a percentage regarded as representing 'rare' species by Thompson *et al.* (2003a). A more realistic comparison of diversity and assemblage similarity is therefore best confined to the more easily recorded lizard species.

The richness of lizards (51 species) from the Abydos/Woodstock area is exceptional and represents the third most speciose lizard assemblage yet reported in Australia. Pianka (1996) recorded 53 species on the Red Sands site in the Great Victoria Desert and Rolfe and McKenzie (2000) recorded 71 species for the Carnarvon Basin survey. James (1994) recorded 40 lizard species on the central Australian study site, which was dominated by *Triodia*. In contrast to the central Australian study and the present one in the Pilbara, Pianka sampled for nearly four years of field time over a 28 year period compared to the 74 days of sampling during the present survey and the 180 sampling days of James (1994). An exceptionally high lizard richness of 57 species has also been documented on Lorna Glen Station in the eastern Gascoyne bioregion (Cowan pers. comm.). The duration of sampling thus plays a very significant role in defining species richness and the use of species accumulation curves has been proposed to define the probable richness of sites sampled over a limited temporal span (Thompson & Withers 2003; Thompson *et al.* 2003b).

The diversity of the herpetofauna in the study area probably reflects the juxtaposition of diverse habitats, such as the extensive areas of *Triodia* spp. grasslands on sandy soils, with isolated rockpiles and breakaways, and also the loamy soils and fringing woodlands of creeks and drainage lines. Forty-one lizard species were recorded from the eight main sampling sites and an examination of relationships between lizard assemblages on sites (Fig 2) provides some support for this proposition. The assemblage on the loams associated with riparian vegetation at WS1 is quite dissimilar to the remaining sites that are located on sands dominated by *Triodia*. Additionally, the site close to a rocky breakaway, WS8, also has a distinct assemblage from those on the surrounding sandy plain. James (1994) recorded between 23 and 32 lizard species at the subsites in central Australia, considerably more than the 17–25 recorded in this study. However, similarity between subsites was high at around 58% (James 1994), such that only 40 species were recorded in total compared to the 41 in this study. Further differences in the two studies occurred in the period of peak activity of reptiles. In central Australia, activity was greater in spring than autumn (James 1994), while on the Abydos Plain activity was greater in late summer than in spring (Table 3). Thompson *et al.* (2003a) contrast species diversity and evenness across 12 subsites (biotopes) at Bungalbin and 10 at Ora Banda, both in the Eastern Goldfields of Western Australia, and indicate that species richness varies from 17 to 26 in the former and 14–28 in the latter. They concluded that "These data indicate considerable variation in reptile assemblages for closely related sites both with and without similar soils and vegetation".

Pianka (1986) suggested that the richness of Australia's arid herpetofauna resulted from the influence of several environmental factors, such as the interdigitating of several habitats, presence of the ubiquitous and unique *Triodia* spp. grasses, a variable and unpredictable rainfall and the replacement of the role of mammalian predators by reptilian taxa. Morton and James (1988) proposed a multi-causal scheme to explain the diversity and abundance of Australian desert lizards that invoked an interaction between climatic, edaphic and (a complex of) biotic factors. Their synthesis was re-examined by Pianka (1989) who evaluated eleven causal factors that made a contribution to the richness of desert lizards, including the role of fire and the biogeographic history of regions. Pianka concluded that many links in Morton and James' causal network were well established, but for others the evidence was weak. Certainly, the role of fire in creating a complex of seral community stages is significant in enhancing lizard diversity (see below).

The reproductive activity of reptiles from the Woodstock/Abydos study area indicated that most species were reproductively active during the spring and summer (How *et al.* 1991) and that reproductive activity may be curtailed when environmental conditions had been unfavourable for many months. How *et al.* (1991) also concluded that the lower incidence of reproductive activity seen in March 1988, compared with subsequent February–March samplings, was the result of a long drought that preceded that sampling. James (1991b) stated that most species of lizard in the central Australian study site reproduced only once during the three year study with most species failing to reproduce in a 'dry' year. It is highly likely that many reptile species in the Pilbara reproduce opportunistically following improved environmental conditions after episodic rainfall events and thus show similar stochastic population responses following rain to those reported by James (1994) in central Australia.

The above average rainfall during the first two summers of this study promoted rapid growth and seeding in *Triodia* spp. and other grasses, while numerous shrubs and trees produced vegetative growth and flowers. The impact of this was to provide visibly improved trophic resources for vertebrates in the form of new plant growth, grass seeds and insect prey, and contrasted with conditions observed at the very beginning and the end of our study period. Amphibians responded almost immediately to the March 1988 deluge and the breeding chorus was extensive over the study area.

The diets of three sympatric *Ctenotus* skinks at Woodstock were examined (Twigg *et al.* 1996) and indicated that, despite a large dietary overlap, two of the species showed dietary separation on a seasonal basis. James (1991a) also showed a seasonal change in diet within species of *Ctenotus* in central Australia that responded to changes in abundance of their main dietary prey. These seasonal shifts in dietary pattern in selected abundant species of lizard could conceivably be extrapolated to less abundant taxa and, when coupled with improved conditions for reproduction, could account for many of the long-term changes in abundance of species in arid study sites. The long-term appraisal of the lizard assemblages in the Great Victoria Desert showed only minor changes in use of resource states by lizards when examined nearly 12 years apart, and although some taxa increased in number between these periods, others declined but the general use of space, diet and time remained similar (Pianka 1986).

Fire has played an important part in structuring arid zone assemblages (Pianka 1989), and at Abydos/Woodstock fire has previously been the focus of considerable research (Suijendorp 1967). However, with knowledge of the regeneration rate in areas burnt in January 1989 and January 1990, it was apparent that at least ten years had elapsed since the major sampling sites were previously burnt. Other studies of the impact of fire on arid zone reptiles (Caughley 1985; Fyfe 1980; Masters 1996) have relied on examining the assemblages in areas burnt at various times prior to the study. In our study the same major sampling sites were monitored for two years before and one year after burning (Table 4).

Pianka (1989) has reviewed the available data on the impact of fire on desert reptile assemblages and concluded that it played a key role in contributing to the richness of lizards. The impact of fire on the lizard fauna of areas subject to intensive sampling on the study area showed a reduction in both the number of species and individuals in burnt areas. Those species best able to survive the short term effects of fire were burrowing or fossorial species. It is not known what the longer term response to fire might be as the study was concluded 10 months after the fire and during one of the driest periods for 20 years when post fire regeneration of vegetation was minimal. Teale (personal observation) has recorded similar initial responses to fire in the Pilbara with burrowing species showing a marked increase in numbers trapped immediately post-fire. These data are in close agreement with the findings of Caughley (1985) who recorded four burrowing species that forage over open ground as the most abundant species in most recently burnt areas of mallee in western New South Wales. The data of Caughley (1985) also indicate that there is a continuous replacement of species as the vegetation passes through successional stages after fire, such that the number of species remains relatively constant.

This study has indicated that there is significant spatial and temporal variation in the lizard community of the Abydos Plain that responds to periodic fluctuations in environmental parameters, habitat differences and fire history. This variation can account for the high diversity of lizards, and by analogy all reptiles, documented for this dominant landscape in the Chichester subregion of the Pilbara bioregion.

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Operational sex ratio and mating behaviour of the myobatrachid frog *Neobatrachus kunapalari*

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Abstract

Matings involving two or more males and a single female (polyandry) are now widely reported in frogs. Polyandry may occur when the sex ratio at breeding sites (the operational sex ratio, OSR) is heavily biased towards males. We report here variation in OSR and the occurrence of polyandrous groupings in the frog, *Neobatrachus kunapalari*. When the OSR had a low male bias conventional amplexed pairs formed with one male and one female. When the OSR was more strongly male biased, groups containing one female and up to seven males formed. At a site with an OSR of 21 females:35 males, mated males were significantly smaller than unmated males but there was no correlation between male and female size in amplexed pairs. We argue that skew in the OSR may favour the facultative appearance of behaviours, *e.g.*, multiple male matings, that raise the risk of sperm competition occurring.

Keywords: operational sex ratio, frogs, amplexus, polyandry, mating behaviour

Introduction

Reports of multiple male frogs in amplexus with a single female occur sporadically in many frog families (Byrne & Roberts 2004). In some cases, these sorts of associations lead to polyandrous fertilisation of eggs from a single clutch (*e.g.*, D'orgeix and Turner 1995; Roberts *et al.* 1999) and polyandry is reasonably suspected in others (*e.g.*, Jennions and Passmore 1993). Many multiple-male, single-female associations in frogs may actually involve a real risk of sperm competition. Byrne *et al.* (2002) reported that the risk of sperm competition was associated with an increase in testis mass in Australian myobatrachid frogs. Their analysis of "risk of sperm competition" was based on a survey of the literature where they extracted data on the likelihood of males coming into close, physical proximity or contact with each other (and females), *e.g.*, as in multiple male amplexus. They found that several *Neobatrachus* species had relatively high testes mass (*N. kunapalari*, testes approximately 0.26% of body mass, range in genus, 0.05 to 1.23% across 10 species, Byrne *et al.* 2002). There are reports of both very dense breeding aggregations (*N. pictus*, Roberts 1978) and multiple-male, single-female aggregations in *Neobatrachus* species (*e.g.*, cover photo of Main 1965 for *N. pelobatoides*) indicating a high risk of sperm competition. In *Crinia georgiana*, density, bias in the operational sex ratio (OSR, ratio of fertilisable females to available males, Emlen and Oring 1977) and the frequency of polyandrous matings are all positively correlated (Byrne & Roberts 2004) suggesting a possible general correlate of polyandry: strong male bias in the OSR leads to males using alternative mating tactics, *e.g.*, group matings, to obtain fertilisations.

Neobatrachus kunapalari is an explosive breeder that breeds after heavy summer and winter rains in the semi-arid region of south-western Australia (Mahony & Roberts 1986; Roberts & Majors 1989). We report here observations of multiple male, single female aggregations in the myobatrachid frog *Neobatrachus kunapalari*, and relate this to variation in the operational sex ratio (OSR) in breeding ponds. We speculate about how variation in OSR might affect mating behaviour in *N. kunapalari*.

Methods

We observed breeding behaviour of *N. kunapalari* at two sites: 13 km north of Kellerberrin on the Trayning Road (16–19 April, 2002) and in a rubbish dump at Hedges, 13 km south south-west of Narembeen (21 February, 1986), both in the semi-arid, grain-growing region of Western Australia. At Kellerberrin, the breeding site was a human-made, clay-lined drainage ditch on gently sloping pastureland, approximately 5 x 1 m and 10 cm deep. Pond water was very turbid and opaque due to suspended clay. Observations were made between 19:00 hrs and 21:00 hrs from 16th April to 19th April, 2002. The Narembeen pond was formed after a heavy, late afternoon-evening thunderstorm. It was a roughly rectangular clay pond approximately 30 m x 5 m x 25–30 cm deep with turbid water. Headtorches with white light were used for making all observations. Amplexed pairs were placed in small plastic containers to collect eggs as they were deposited. Snout-vent length of all frogs collected at Narembeen were measured. At both sites all frogs collected were considered mature. For males this was based on the presence of nuptial pads and/or calling activity. Frogs considered female were carrying mature eggs, lacked nuptial pads, were depositing eggs or they were in amplexus and from their size they appeared gravid. We have never observed small, immature frogs of any *Neobatrachus* species in ponds where breeding was taking place despite a considerable amount of field work on all species in this genus (Roberts 1997a,b).

Data are presented as means ± standard errors with an α of 0.05 used throughout.

Results

Field Observations

Kellerberrin: on the 16th April 2002, there was a heavy rainfall event that produced 13.5 mm of rainfall in 24 hours. Subsequently, we observed a large breeding chorus where males were calling both in the water and from the damp ground surrounding the pond. From 19:00 to 19:30 h, we observed four single-male matings. From 20:00 – 21:00 hrs, we observed three separate, multiple-male amplexus events comprising five, six and seven males respectively, trying to amplex a single female. In each multiple-male amplexus, one male was in inguinal amplexus, one male around each of the front legs, and the remaining males were vying for position underneath and alongside the other males (Figure 1). On the following night (17th April), after a further 7 mm of rain, during two hours of observation, we saw two single male matings. On the third night (18th April), we observed three single male matings. By the fourth night (19th April) all breeding activity (calling and mating) had ceased and the pond contained numerous egg masses. There was a strong bias to males on 16th April but this was drastically reduced on the following two nights (Table 1).

Narembeen: this pond was observed from 00:30 hrs to 03:30 hrs. At 00:30 hrs there was one amplexed pair. Other pairs formed over the next three hours. Seventeen pairs, four unamplexed females and eighteen unamplexed males were collected between 03:00 hrs and 03:30 hrs (close to dawn: a total of 21 females, 35 males). Sixteen conventional single male, single female pairs formed. A seventeenth pair was approached and touched by a calling male but the calling male did not make any obvious attempt to amplex or displace the amplexed male. The caller left and resumed calling.

At Narembeen, mated males had significantly smaller snout-vent lengths than unmated males (t_{33} = 2.203, p = 0.035; mated males 59.23 mm ± 1.01; unmated males, 62.22 mm ± 0.91). The correlation between snout-vent lengths of mated males and females was not significant (r = 0.150, p > 0.05). The number of eggs deposited per pair averaged 918 ± 102 with a range from 28 to 1616. We do not know whether females were depositing eggs before pairs were collected so the average may be an underestimate of actual fecundity if there were some incomplete clutches (*e.g.*, the low of 28).

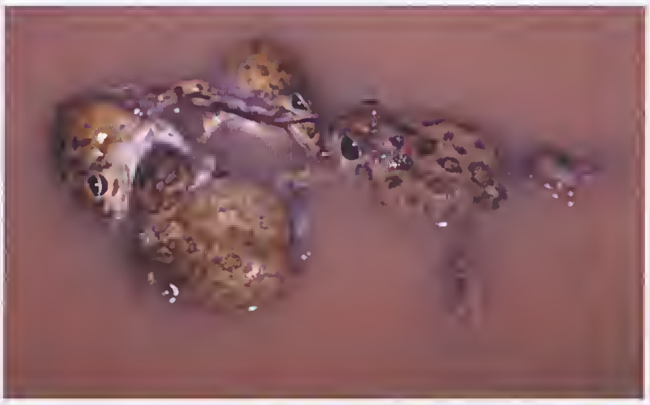

Figure 1. Amplexed group: one female and four males, Kellerberrin. The head and limbs of the female are obscured but her abdomen is visible between the two males on the left.

Operational Sex Ratios

Operational sex ratios and frequencies of multiple male matings are given in Table 1. For the first night at Kellerberrin we calculated separate OSR values for observations from 19.00 – 19.30, and those made between 20:00 hrs – 21:00 hrs, because females were not marked and we could not determine whether the same females were amplexed at both time periods. To calculate the OSR we assumed all frogs present in the pond at the time of observation were available to mate as all females appeared gravid and most males were calling.

Discussion

Our observations document polyandrous mating aggregations that might lead to multiple paternity of single egg clutches in *N. kunapalari*. Our data are consistent with an increased frequency of multiple-male, single females aggregations when the OSR is more heavily male biased if we assume the early data from 16th April reflect initial pairing that is modified over time (Table 1). Our observations are comparable to the multiple-male amplexes in *N. pelobatoides*, illustrated on the cover of Main (1965). We did not follow amplexed pairs through the process of egg deposition and the extra

Table **1**

Sex ratio and frequency of single- and multiple-male matings in breeding choruses of *N. kunapalari*.

	Kellerberrin				Narembeen
	16/4/2002		17/4/2002	18/4/2002	21/2/1986
	19.00–19.30	*20.00–21.00*			
Males	32	32	28	26	35
Females	4	4	15	14	21
OSR	0.125	0.125	0.54	0.54	0.6
Number single matings	4	0	2	3	17
Matings with > 1 male	0	3	0	0	0
% Matings with > 1 male	0	100	0	0	0

males may leave the mating assemblages before eggs are released or never release sperm. Demonstrations that additional males release sperm would require direct collection of sperm, *e.g.*, using condoms (Hettyey & Török 2004), or genetic determination of extra-pair paternity.

Apart from attempting to obtain fertilisations, what else could attendant males be doing? Males may be trying to displace other males and gain exclusive fertilisation but the pairing success of smaller males at Narembeen suggests this is unlikely as we would expect larger males to win fights leading to a large male advantage. In *Bufo bufo*, fighting and displacement of amplexed males over several days shifts the population from initially randomly paired by size to positive, size assortative mating, particularly because large males displace smaller males amplexed with larger females (*cf.* Davies & Halliday 1977). The lack of a significant correlation between the size of mated males and females in *N. kunapalari* also argues against displacement leading to more effective fertilisation in pairs with better matched body sizes (*cf.* Davies & Halliday 1977), as some pairs were likely to already be depositing eggs.

Assuming males release sperm sometime during egg deposition, the frequency of multiple male matings in *N. kunapalari*, 21.5% over two sites, is much lower than in *C. georgiana* where 43.5 % of matings involve two or more males (Roberts *et al.* 1999). Our data suggest that attempts at multiple male amplexus may be a facultative response to male bias in the operational sex ratios as multiple male single females aggregations only occurred when the OSR was strongly male biased (Table 1). This also occurs in *C. georgiana* where the frequency of multiple-male matings and the number of males per mating both rise with increasing male bias in the OSR (Byrne & Roberts 2004). Sullivan *et al.* (1995) describe variations in mating behaviour with increasing density in several frog species. At higher densities males are more mobile and less likely to call to attract mates but they did not report multiple-male, single female amplexes but in these examples it was not clear how density and OSR co-vary. In *C. georgiana*, male bias in OSR and density are positively correlated (Byrne & Roberts 2004).

The comparative analyses of testes mass reported by Byrne *et al.* (2002) suggested the real possibility of sperm competition increasing testes mass in many species. However, the mechanism of sperm competition was not clear: it may be direct competition as in *C. georgiana* (Roberts *et al.* 1999) or by more diffuse competition as suggested for *Rana temporaria* (Laurila and Seppa 1998) and *Bufo americanus* (Kaminsky 1997). In *N. kunapalari*, males amplexed in unconventional positions may release sperm that are sufficiently mobile to achieve at least some fertilisations.

Our data for *N. kunapalari* are preliminary but are consistent with studies on other frogs where increasing chorus density and increasing male bias in the OSR are correlated with shifts in male mating tactics (Byrne & Roberts 2004). Our data also are quantified, natural history observations (rather than anecdotes), coupled with specific data on sperm release or multiple paternity, needed to determine whether sperm competition is relatively common in anurans (as suggested by several recent authors, *e.g.*, Halliday & Verrel 1984; Halliday & Tejedo 1995, Roberts *et al.* 1999, Byrne *et al.* 2002). Ideally, future studies will experimentally manipulate OSR and follow amplexed pairs until egg deposition is complete to test our interpretations.

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Land Birds on Barrow Island: Status, Population Estimates, and Responses to an Oil-field Development

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Abstract

A census of land birds on Barrow Island, Western Australia was carried out during September and October 2001. A total of 178 transects was conducted in six major vegetation zones, with 777 individuals of 16 species of birds recorded. The six most common species, in order of their abundance, were Spinifexbird (*Eremiornis carteri*), White-winged Fairy-wren (*Malurus leucopterus*), Singing Honeyeater (*Lichenostomus virescens*), White-breasted Woodswallow (*Artamus leucorynchus*), Zebra Finch (*Taeniopygia guttata*), and Welcome Swallow (*Hirundo neoxena*). Our total population estimates for these species were generally comparable to those of a survey of Barrow Island in 1976 (Sedgwick 1978), but some differences existed for these and other species. In an analysis of habitat preferences, more complex vegetation zones supported more species. The density of both Spinifexbirds and Singing Honeyeaters was significantly correlated with the number of emergent shrubs. Also, across vegetation zones, the number of different bird species was correlated with the maximum height of vegetation in a habitat. Species richness and numbers of individuals were compared between natural areas, areas surrounding oil pads, and along roadsides. There was no significant difference in species richness across these three areas, but there was a significant increase in number of individuals along road sides. This latter result occurred because disturbed areas along roadsides were colonized by a large species of spinifex, *Triodia angusta*, which supported greater numbers of birds than other species of spinifex away from roads. The oil-field development on Barrow Island occupies approximately 4% of the land area on the island and appears, at present, to have had a relatively minor impact on the populations of land birds. This conclusion is qualified in that several species of insectivorous birds have declined in numbers over the last 25 years, and the reasons for these declines are not yet known.

Keywords: birds, Barrow Island, oil-field development, species diversity

Introduction

Barrow Island is the second largest island (after Dirk Hartog Island) in Western Australia. Barrow Island experiences a tropical arid climate, and its vegetation is dominated by spinifex (*Triodia* sp.). The ecosystem on Barrow Island is interesting because it has been relatively unimpacted by the negative consequences of human activity and development, a situation unique in Australia and elsewhere. Barrow Island was designated as a Class A Reserve in 1910, which greatly limited human activity. In 1964 an oil-field development began on the island (by Western Australian Petroleum (WAPET), and continues with Chevron Inc. Despite this, however, there are no introduced animal species on the island, the fauna has never been persecuted or hunted, and the terrestrial vertebrates are extremely common.

The avifauna on Barrow Island was surveyed three times during the 20th century: by F. Lawson Whitlock in 1917 and 1918 (Whitlock 1918, 1919), by D. L. Serventy and A. J. Marshall in 1958 (Serventy and Marshall 1964), and by E. H. Sedgwick in 1976 (Sedgwick 1978). Additionally, W. H. Butler has made extensive and long-term observations of the avifauna on Barrow Island beginning in 1964 and continuing to the present. During this collective work, a total of 113 bird species has been recorded (110 species listed by Sedgwick (1978) plus three additional species recorded by Butler (pers. comm.), and 32 species have been recorded breeding there. Additional work on the avifauna of Barrow Island consisted of an analysis of the diet of insectivorous birds (Wooller and Calver 1981) and a study of breeding chronology (Ambrose and Murphy 1994).

Given the approximate 25 years since the survey by Sedgwick (1978), we sought to conduct a current survey of land birds on Barrow Island, with three objectives: 1. to quantify the occurrence and abundance of species; 2. to document any changes in the avifauna since the survey of Sedgwick (1978); and 3. to quantify the effects of the oil-field development on the island's land birds. Our focus on land birds differs from the complete avifaunal survey of Sedgwick (1978), and this earlier research remains the primary source for a list of all bird species recorded on the island. We focused on land birds because our time on the island was limited and we wanted to obtain an accurate estimate of population densities. We acknowledge that oil-field development can have both direct and indirect consequences for water birds and sea birds as well as land birds but our focus here is only with the island's land birds.

Study area and methods

Study area

Barrow Island (20°43'S, 115°28'E) is a continental island, 56 km from the Western Australian coast between Onslow and Port Hedland, and approximately 1300 km north of Perth. It has been isolated from the mainland for 7500 to 8000 years. It was formed from Tertiary limestone, and consists of high coastal cliffs on the west, sloping down through central uplands to coastal plains on the east. The climate is classified as tropical arid, or as a northern monsoonal climate (Gentilli 1972), with seasonally extremely high temperatures (> 45°C), and sporadic and highly variable rainfall. The rainfall averages 330 mm, but in four out of five years, the rainfall averages just 20% of this value. Most of the annual rainfall occurs during cyclones between February and June. Creeks and claypans will hold fresh water after a cyclone, but otherwise freshwater is extremely limited. Heavy dews, however, occur throughout the year (Buckley 1983) and provide a source of fresh water for birds, as do shoreline seeps. Additionally, facilities associated with the oil-field development now contain standing fresh water.

Vegetation on Barrow Island has been studied by several investigators. Butler (1970) identified six major vegetative zones, and Buckley (1983) identified nine major zones, with 29 subtypes. On contract from WAPET, Matiske Consulting Group produced a detailed vegetation map of the island, identifying six major terrestrial vegetation types and 31 subtypes (excluding marine and two tidal vegetation zones). Our work and analyses were based on this latter map. A digital version of this map was available from National Geographic Information Systems (NGIS, Perth, Western Australia), and under contract, NGIS produced a field map of the vegetation zones for our use and calculated the area occupied by each zone, as well as areas occupied by various types of development (roads, oil wells, etc.).

Briefly, the six land forms/vegetation units were: coastal complexes and dune systems (type C in Table 1, creeks or seasonal drainage lines (D), flats (F), limestone ridges (L), clay pans (S), and valley and escarpment slopes (V). *Triodia* hummock grassland is the dominant vegetation type and *Triodia* sp. occurs over 93% of the island. A complete list and description of each vegetation type, and subtype, is available on request from the authors.

Because we wanted to calculate total population densities for the common land birds, we needed to calculate the total habitat area (land area) available to birds on Barrow Island. To do this, we corrected each vegetation zone for the area in each zone that was taken up by the presence of roads, oil pads, etc. We corrected the area measurements as follows: the total area of Barrow Island is 23 452.9 ha (measured from the high tide mark). Of this area, 161.3 ha (0.69%) consist of bare sand, marine and tidal habitats (which were not censused and in which there were no disturbances), or large areas with no vegetation, such as the airport and main Chevron camp. This leaves a total area of 23 291.6 ha encompassing the six major vegetation zones surveyed in this study, and also the area in which all of the disturbances associated with the oil-field development were located (excluding the airport and camp). The total area of disturbed areas (again excluding the airport and camp) is 915.7 ha or 3.93% of the total area. This includes the area occupied by 821 oil wells (as of 1997), and approximately 550 km of roads. In correcting the areas of each vegetation zone, we reduced the area by 3.93% to account for the disturbance in that zone. We recognize that this correction makes the assumption that disturbances are distributed randomly across vegetation zones, which is not correct. It would be logistically impossible to precisely calculate how much of each vegetation zone is disturbed, however we believe that our correction provides as accurate a calculation of the available habitat area as is possible. We also fully recognize that land birds do use roads and other man-made structures (although no birds were seen to use oil wells as 'habitat'). Nevertheless, our correction of the area of each vegetation zone by the amount of disturbed area within that zone seemed to us as the most conservative solution in order to calculate overall population estimates.

Methods

Fieldwork was conducted from 14 September 2000 to 12 October 2001. A census was carried out on birds via transects in quadrats in each of the 31 vegetation zones. Our initial goal was to carry out a census in six quadrats within each vegetation zone, but in some cases this was not possible because some habitats were limited in area. Although the quadrats were located in specific vegetation zones, we made a concerted effort to census birds in all areas of the island. A total of 178 quadrats were censused.

The transect counts were conducted each morning, weather permitting, from 0545 to 1100 and again from 1500 to 1700. The quadrats were 2 ha in size, and in most cases were 200 m long X 100 m wide. The length of the quadrat was determined using a portable GPS unit (Garmin 45; accuracy = 10 m). The width of the quadrat was estimated visually. In order to maintain accuracy, both observers practiced estimating 50 m lengths and then checked these distances with a tape measure. We surveyed each quadrat together. One of us walked slowly in a straight line down the middle of the quadrat, and the other person zigzagged through the quadrat, intersecting the path of the person walking straight every 50 m. All birds seen or heard inside the quadrats were counted. Each individual bird that was recorded was noted by both observers to ensure that it was only recorded once. A census was carried out in each quadrat only once, and all censuses took approximately 10 min to conduct (range 9–13 min).

The exceptions to our methods as described above were as follows: first, in narrow, and linear vegetation zones, *e.g.*, coastal habitats, the transects were 400 m long and 50 m wide; second, in habitats with dense and large spinifex both observers walked straight lines through the quadrats in parallel lines 40 m apart.

As most vegetation zones were characterized by low plant height, and discontinuous distributions of plants, all bird species were equally detectable and we believe that we counted all birds using the quadrats. In areas with continuous and dense spinifex, the spinifexbird was sometimes difficult to detect because it often hid within large spinifex plants. In such situations, it was possible that we missed a few individual spinifexbirds although we made every effort possible to detect all individuals present.

We calculated total population estimates for all 16 species recorded on transects (see Results). The estimates were made as follows: (population density in each vegetation zone)/(proportion of total area of each zone that was surveyed during quadrat transects), summed over all vegetation zones = total population estimate.

Besides conducting transects in natural, undisturbed areas, we also carried out a census of birds around oil pads (the raised or leveled areas on which there was a Lufkin oil pump) and also along roads. The oil pad and road censuses were conducted as described above, with the following exceptions: first, the oil pad quadrats consisted of abutting rectangles at right angles to each other (either two or three, two ha total area) that were oriented so that they surrounded the oil pad; and second, the road side quadrats consisted of two areas 200 m long x 50 m wide (two ha total area) on either side of the road. For the roadside transects, censuses were carried out in both areas on either side of the road simultaneously, with each of us walking along a mid-line of the quadrat. The oil pad and road transects were conducted in four vegetation zones as follows: L1 (hummock grassland of *T. wiseana* with *Ficus platypoda* on central limestone ridges); L3 (hummock grassland of *T. wiseana* with low mixed shrubs including *A. gregorii* on limestone ridges); L7 (hummock grassland of *T. wiseana* with dense pockets of *M. cardiophylla* on limestone ridges); and V1 (hummock grassland of *T. wiseana* with mixed emergent shrub species on valley slopes). These four habitats were chosen because they were the most common habitats on the island and because the majority of oil pads and roads associated with the oil-field development were located in these habitats.

We took vegetation measurements on each quadrat to quantify large-scale differences between vegetation types. At the starting point of each transect, and at every 50 m (5 points total) we measured vegetation cover and vegetation height. Vegetation cover was measured at ground level and was scored as the number (percentage) of 1 cm squares of a 1 m long stick that was covered by living vegetation. In addition, for the entire quadrat as a whole, we measured the height of the tallest tree or shrub (maximum vegetation height) and also counted the number of emergent shrubs. Emergent shrubs were defined as woody shrubs that were at least 50% taller than the surrounding vegetation. This relative measure was necessary because the height of the spinifex, which covered the ground in most areas, varied greatly in height (e.g., from 0.3 m for *T. wiseana* to 1.5 m for *T. angusta*). The number of emergent shrubs was scored as 1 (0 emergent shrubs), 2 (1–10 emergent shrubs), 3 (10–25 emergent shrubs), 4 (25–50 emergent shrubs), and 5 (50+ emergent shrubs).

In addition to counting birds on the quadrats, we also recorded birds seen outside the quadrats during the formal counts, and also during general fieldwork during our time on the island.

Results

Avifauna

During transects, 777 individuals of 16 species were recorded. Two additional species, the Black-shouldered Kite and Richard's Pipit (see below) were observed during general fieldwork, but not recorded on transects. An assessment of the status of each of these 18 species is presented below. Our definitions of status is: common = an abundant species (>10 individuals recorded on quadrats), seen in many habitats across the island; uncommon = a species only occasionally seen (3–10 individuals recorded on quadrats), or restricted to specific habitats; rare = a species for which just a few individuals were seen (1–2 individuals recorded on quadrats), and/or a species that was restricted to just one or two habitat types.

- Spotted Harrier (*Circus assimilis*): Uncommon; individuals occasionally seen inland; scattered along coast.
- Brahminy Kite (*Haliaster indus*): Rare; pairs occasionally seen inland off the quadrats; scattered along coast.
- Osprey (*Pandion haliaetus*): Rare on quadrats; pairs regularly spaced around coastline; not seen inland but we received reports that individuals will cross the island (W. H. Butler, pers. comm.). All individuals we recorded were seen within 1 km of the coastline. Nesting pairs were observed using both natural sites and nesting platforms erected by WAPET.
- White-breasted Sea-Eagle (*Haliaeetus leucogaster*): Rare on quadrats; pairs occasional along coastline; not seen inland, but we received reports that individuals regularly hunt inland especially near hills (W. H. Butler, pers. comm.). Nesting pairs seen on southern coast.
- Black-shouldered Kite (*Elanus caeruleus*): Rare; not seen on quadrats; two individuals seen on island during fieldwork.
- Australian Kestrel (*Falco cenchroides*): Rare; individuals occasionally seen inland; not seen along coast, although this species is known to nest on coastal cliffs (W. H. Butler, pers. comm.).
- Bar-shouldered Dove (*Geopelia humeralis*): Common in central limestone ridges in valleys, less so on flats and in coastal area; known to nest on limestone ledges, caves, in mangroves and *Acacia* sp. along the coast (W. H. Butler, pers. comm.)
- Black-eared Cuckoo (*Chrysococcyx osculans*): Rare, but scattered throughout island in habitats with emergent shrubs and trees.
- Horsfield's Bronze-Cuckoo (*C. basalis*): Uncommon, but scattered throughout island in habitats with emergent shrubs and trees.
- Sacred Kingfisher (*Todiramphus sanctus*): Rare; only seen along creeks and drainage lines.
- Welcome Swallow (*Hirundo neoxena*): Common and widespread; common around developed areas, less so elsewhere. Many nesting pairs observed at camp and airport.

- Tree Martin (*H. nigricans*): Rare; only one individual seen.
- Australian Pipit (*Anthus australis*): Rare; not seen on quadrats; seen on two occasions in low limestone ridges along coast.
- Spinifexbird (*Eremiornis carteri*): Common; the most abundant species on island; in all habitats with spinifex. Many pairs were breeding.
- White-winged Fairy-wren (*Malurus leucopterus*): Common; abundant in most habitats, especially those with complex vegetation structure. Many pairs were breeding.
- Singing Honeyeater (*Lichenostomus virescens*): Common; abundant in all habitats with dense vegetation or with emergent shrubs and trees. Many pairs were breeding.
- Zebra Finch (*Taeniopygia guttata*): Common on clay pans; uncommon in other habitats.
- White-breasted Woodswallow (*Artamus leucorynchus*): Common; abundant in all habitats with dense vegetation or with emergent shrubs and trees.

In Table 1 we list, for each of the six land forms/vegetation units, the number of species and individuals recorded, as well as the estimated densities of the six common species. Across all vegetation types together, the density of birds averaged 2.20 birds/ha. Across the 31 vegetation types, there was a significant correlation between the area of habitat that we surveyed and the total number of species ($F_{1, 29} = 11.585$, $R^2 = 0.261$, $P = 0.002$) and total number of individuals ($F_{1, 29} = 79.588$, $R^2 = 0.724$, $P < 0.001$) recorded. Similarly, there was a significant relationship between the total number of species and number of individuals recorded on the transects ($F_{1, 29} = 36.289$, $R^2 = 0.541$, $P < 0.001$).

Total population estimates for all 16 species recorded on quadrats are presented in Table 2, along with the population estimates for these same species published in Sedgwick (1978).

Habitat Relations

Land birds were distributed across the entire island, but both species diversity and abundance varied with habitat (Table 1). Each of the common species observed in this study was found in a variety of habitats, but densities varied considerably (Table 1).

For the 31 vegetation types separately, we examined whether any of the habitat variables correlated with number of species and individuals recorded, and with the densities of the six common bird species (Table 1). A complete summary of habitat measurements and species abundances on each of the 31 vegetation subtypes is available on request from the authors. There was no significant correlation between any of the habitat variables and species richness, or total number of individuals. Nevertheless, several significant relationships between habitat measurements and densities of individual species emerged: the density of Spinifexbirds was significantly correlated with the mean emergent score ($F_{1, 29} = 11.046$, $P = 0.002$) and with vegetation cover ($F_{1, 29} = 5.393$, $P = 0.027$; Fig. 1). The density of Singing Honeyeaters was significantly related

Table 1

Summary of quadrat results and densities of the six most common passerines.

Vegetation			Birds recorded		Densities of most common species (birds/ha)					
Type	Area on island (ha)	Area surveyed (ha)	Species	Number	Spinifexbird	White-winged Fairy-wren	Singing Honeyeater	White-breasted Woodswallow	Zebra Finch	Welcome Swallow
C-coastal complex and dune systems	1,473.8	56	10	169	1.43	0.48	0.64	0.12	0.07	0.16
D-Creeks or drainage lines	1,089.9	18.6	9	56	1.29	0.59	0.27	0.22	0.22	0.22
F-Flats	3,865.5	58	9	144	1.38	0.24	0.33	0.26	0.05	0.16
L-Limestone ridges	9,067.6	164	12	297	1.07	0.37	0.19	0.05	0.02	0.02
S-Clay pans	185.6	10.9	6	47	0.37	0.46	0.18	0.64	1.65	0.01
V-Valley slopes and escarpment slopes	6,693.2	46	4	64	0.89	0.30	0.17			
TOTALS	22,375.60	353.5	16	777	1.14	0.37	0.29	0.12	0.09	0.10

Table 2

Number of individuals of each species recorded on quadrats and total population estimates for Barrow Island in comparison with the estimates of Sedgwick (1978).

Species	Quadrat counts	Total population estimate based on this study	Population estimate from Sedgwick (1978)
Spotted Harrier	3	162	180
Brahminy Kite	2	23	15
Osprey	1	73	180
White-breasted Sea-Eagle	1	73	3
Australian Kestrel	1	69	1,650
Bar-shouldered Dove	14	692	180
Black-eared Cuckoo	2	67	No estimate
Horsfield's Bronze-Cuckoo	5	102	910
Sacred Kingfisher	1	6	12
Welcome Swallow	36	1,077	8,500
Tree Martin	1	6	7,050
Spinifexbird	404	24,623	17,800
White-winged Fairy-wren	132	7,519	8,150
Singing Honeyeater	101	3,920	3,050
Zebra Finch	32	1,152	No estimate
White-breasted Woodswallow	41	1,945	3,450

to maximum vegetation height ($F_{1,29}$ = 10.913, P = 0.025) and to the mean emergent score ($F_{1,29}$ = 5.860, P = 0.022).

We combined data from each of the six major habitat zones to examine broad scale habitat relationships within the avifauna. We compared species number, total number of individuals, and mean bird density across these six habitat zones according to each of the habitat variables. The number of species recorded in each habitat was significantly correlated with maximum vegetation height (Spearman Rank Correlation R_s = 0.929, P = 0.038) but no other significant correlations were observed.

Effects of Oil-field Development

Our study of the effects of the oil-field development was limited to four vegetation zones as described in Methods: three limestone ridge habitats (L1, L3, and L7) and one valley habitat (V1).

We first examined whether within each of these habitat types, the vegetation differed between natural areas, around oil-pads, and along roadsides. Within habitat L1, there was significant variation in vegetation cover between these areas ($F_{2,87}$ = 4.363, P = 0.016), with natural areas supporting significantly lower vegetation cover than either the areas around oil-pads (P = 0.027) and along roads (P = 0.006); vegetation cover did not differ significantly between oil-pads and along roads. No other difference was detected within habitat L1. In both habitats L3 and L7, there were no significant differences in vegetation measurements across the three areas. In habitat V1, there was significant variation in the number

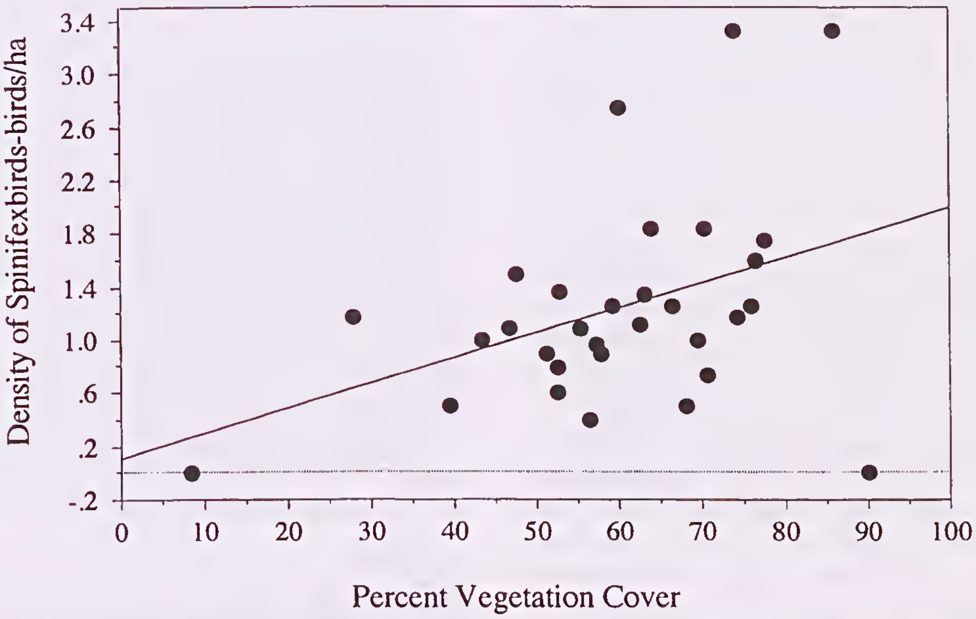

Figure 1. Relationship between mean percent vegetation cover in habitats and the density of Spinifexbirds. The correlation is statistically significant (see text).

of emergent shrubs on quadrats ($F_{2,15} = 3.961$, $P = 0.042$), with natural areas having more emergents than the areas around oil-pads ($P = 0.0132$). Also, mean vegetation height differed significantly between the three areas ($F_{2,87} = 8.724$, $P = 0.004$), with vegetation in natural areas significantly taller than around oil-pads ($P = 0.0002$) and along roads ($P = 0.0013$). Thus, comparison of vegetation measurements between natural and disturbed areas varied with the specific habitat type.

The census results conducted in the four vegetation zones were analyzed in two ways. First, across the four vegetation zones, there was no significant variation in either the number of species ($F_{3,8} = 1.961$, $P = 0.198$) or number of individuals ($F_{3,8} = 1.620$, $P = 0.620$) recorded according to area sampled (natural areas, oil-pads, roadsides). Second, we asked whether, regardless of vegetation zone, species richness and number of individuals varied between natural areas, oil-pads, and roadsides. Although there was no significant variation in number of species recorded ($F_{2,9} = 0.864$, $P = 0.454$), there was significant variation in number of individuals recorded ($F_{2,9} = 4.922$, $P = 0.036$). Roadsides supported significantly greater numbers of individuals than natural areas ($P = 0.013$) and oil-pads (although not significantly so, $P = 0.077$). The number of individuals did not differ significantly between natural areas and oil-pads ($P = 0.301$).

Discussion

Avifauna

Of the 110 bird species recorded on Barrow Island and reported by Sedgwick (1978), 48 were land birds. These 48 species included 15 permanent residents, six regular migrants, and 27 irregular visitors. Of the 15 species that Sedgwick considered to be residents, the only species that we did not observe was the Southern Boobook (*Ninox novaeseelandiae*). Our quadrat counts were conducted during daylight hours and thus it is not surprising that we not detect this species on the quadrats. Nevertheless, we did do considerable driving at night, and this species was neither heard nor observed. Additionally, W. H. Butler (pers. comm.) reports that the Southern Boobook is no longer resident on the island. Of the 18 species that we recorded, four species were considered by Sedgwick to be non-residents: the Zebra Finch and Black-eared Cuckoo were considered to be irregular visitors, and the Horsfield's Bronze Cuckoo and Sacred Kingfisher were considered to be regular migrants. Considering these species in turn, the Zebra Finch now appears to be a regular migrant to the island and breeds there every year (L. McClements, pers. comm.). The Black-eared Cuckoo is now known to be an irregular migrant, and Horsfield's Bronze Cuckoo a regular migrant (W. H. Butler and R. Johnstone, pers. comm.). Both species are widespread on the island during the breeding season, and both undoubtedly commonly breed there (see Pruett-Jones and Tarvin 2001). We have no observations or other information to contradict the status of the Sacred Kingfisher as a regular migrant.

Sedgwick recorded four other species as regular migrants that we did not observe: the Pallid Cuckoo (*Cuculus pallidus*), the White-throated Needletail (*Hirundapus caudacutus*) which is listed as the Spine-tailed Swift in Sedgwick (1978), the Fork-tailed Swift (*Apus pacificus*), and the White-winged Triller (*Lalage tricolor*). Records of these species have been scattered since ornithological observations on Barrow Island began and none of these species were recorded by Whitlock (1918, 1919) or Serventy and Marshall (1964). It appears that the Pallid Cuckoo and White-winged Triller are both passage migrants to Barrow Island and the two swift species irregular visitors from Asia (R. Johnstone, pers. comm.).

All other land birds listed by Sedgwick and not observed during this study or discussed above (25 species total) are irregular visitors and do not breed on Barrow Island. This list includes some species that could occasionally breed on the island (e.g., Whistling Kite (*Haliaster sphenurus*) and Wedge-tailed Eagle (*Aquila audax*; the record by Sedgwick is now thought to be a mis-identified juvenile White-breasted Sea-Eagle)) as well as species that are accidental occurrences on the island and do not breed there (e.g., Galah (*Cacatua roseicapilla*) and Little Corella (*C. pastinator*)). The number of such accidental species visiting the island or blown over to the island during storms will likely increase as observations continue on the island.

Sedgwick (1978) calculated total population estimates for all of the species he recorded on his quadrats, as did we in this study (Table 2). There are several points of comparison to make. First, we concur with Sedgwick that the estimates for the Osprey are too high. This is a maritime species that can be seen from inland habitats, but inland habitats such as is available on Barrow Island cannot be considered as regular habitat of this species. At the time of Sedgwick's survey, 23 Osprey nests were known on the island, and although we did not attempt to count Osprey nests we suspect that there are approximately this number of active nests still present. Similarly, we believe our estimate of the total population of White-breasted Sea-Eagle is too high, for the same reasons as outlined above. At the time of Sedwick's survey, six sea-eagle nests were known on the island, and during our work we had reported to us the locations of five nests. More accurate population estimates for the Osprey would be approximately 50 birds and for the White-breasted Sea-Eagle, 10–12 birds.

For the three most common species (Spinifexbird, White-winged Fairy-wren, and Singing Honeyeater), our total population estimates and those of Sedgwick (1978) are comparable (Table 2). For many of the other species, there are striking differences. In some cases these differences are easily explainable. For example, the Zebra Finch is clearly now more common on Barrow Island than it was during the work of Sedgwick (W. H. Butler, pers. comm.), as reflected in our results and estimates. Also, if resident numbers of the migratory Black-eared Cuckoo and Horsfield's Bronze Cuckoo fluctuate from year to year, the differences between our estimates and those of Sedgwick (1978) may reflect annual variation in the size of breeding populations.

For other species listed in Table 2, the differences between our estimates and those Sedgwick appear to reflect population declines. The most striking example is the Tree Martin, listed by Sedgwick as the fourth most abundant species on the island (but see Storr 1984), and yet we recorded just one individual on our quadrats. This species, and two other aerial insectivores (Welcome Swallow and White-breasted Woodswallow) appear to have declined in numbers. Assuming this trend relates to insect abundance, it is not yet clear whether it is a short-term trend reflecting annual variation in insect populations or a long-term trend, with broad ecological implications. If, on Barrow Island, the diet of Australian Kestrels is primarily insectivorous, it could be said that a total of four insectivorous species have shown population declines. Notably, however, the three most abundant species (Spinifexbird, White-winged Fairy-wren, and Singing Honeyeater) are either obligatory or primarily insectivorous, and the populations of these species have not declined (Table 2).

Despite the distance of Barrow Island from the mainland, and the relatively long time it has been isolated, there is only one endemic subspecies of bird that resides there, the White-winged Fairy-wren (*M. l. edouardi*, Ford 1987; Schodde and Mason1999) and genetic analysis (Driskell et al. 2002) has confirmed the genetic basis of this subspecific designation. Another unique subspecies of the White-winged Fairy-wren (*M. l. leucopterus*) is found on Western Australia's largest island, Dirk Hartog Island. Wooller *et al.* (1985) suggested that the Barrow Island population of the Singing Honeyeater may be an endemic subspecies, based on vocalizations and measurements, but Schodde and Mason (1999) did not separate the Barrow Island population from the mainland subspecies *L. v. sonorous*, although the basis for that decision is unclear. No genetic analysis of Singing Honeyeaters from Barrow Island has been conducted.

Habitat relations

In this study we did not examine specific habitat preferences of individual species, but rather broad differences in habitat types and how these related to species richness and abundance of birds. All habitat types on Barrow Island, with the exception of clay pans, drainages, and coastal areas are dominated by spinifex. All species that regularly feed on the ground or in vegetation, e.g, Spinifexbird, Singing Honeyeater, and White-winged Fairy-wren, used spinifex plants, but these species also seemed to prefer habitats in which spinifex was interspersed with shrubs and trees. Across habitat types, species richness was correlated with maximum vegetation height, indicating that more structurally diverse habitats supported more species. Furthermore, Spinifexbirds were more abundant in areas with greater cover and more emergent shrubs, and Singing Honeyeaters were more abundant in areas with taller vegetation. Spinifexbirds preferred the densest vegetation of any of the species, and rarely emerged from the spinifex. The greater density of Spinifexbirds in areas with emergent shrubs may be related to variation in insect abundance in areas of greater plant diversity.

Effects of oil-field development

The effect of the oil-field development on land birds on Barrow Island is difficult to accurately assess in a short-term study such as ours. Approximately 4% of the land area on Barrow Island has been altered, but this has had both positive and negative effects on the land birds. Positive effects include more nesting sites for some species (*e.g.*, swallows and woodswallows nesting on buildings, ospreys nesting on utility poles) and increased availability of fresh water for some species (*e.g.*, Zebra Finches), whereas negative effects include loss of habitat, altered habitat around man-made structures, *etc.*

In our comparison of species diversity in natural areas and altered areas, habitat along road sides supported more individuals (but not more species) than natural areas. We believe the reasons for this difference had to do with the effects of disturbance in a *Triodia* dominated habitat. When an area was disturbed, it appeared that the largest species of *Triodia* on Barrow Island, *T. angusta*, rapidly colonized the disturbed area, often times regardless of the dominant surrounding vegetation. For example, in limestone ridge areas, where the small (approximately 0.3–0.5 m high) *T. wiseana* dominated natural vegetation, along the roads there was a two to three m wide area on either side of the road where *T. angusta* occurred, often up 1.5–2.0 m high. Larger, and denser *T. angusta* provided suitable habitat for more individual birds.

As a Class A Nature Reserve, no camping or landing by boaters is allowed on Barrow Island. The only allowed human activity on the island is that associated with the oil-field development and the present leaseholder (Chevron Inc.) controls all human activity on the island. To date, that control and strict quarantine practices for people and vehicles traveling to the island, has acted to protect the Barrow Island ecosystem. Barring the obvious possibility of a damaging oil spill, the avifauna on Barrow Island and the ecosystem itself should continue in its relatively undisturbed condition. When the oil-field is decommissioned, which is likely within the next 10–20 years, the decision on the future of Barrow Island will obviously set the stage for any possible future changes. Given the unique ecosystem on the island, great care should be taken to insure that no future human activity threatens the island.

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Coppice treatment gives hope to a rare and endangered mallee eucalypt in the south-west of Western Australia

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Abstract

Eucalyptus phylacis is a critically endangered mallee eucalypt known from a single clonal population of 27 ramets in the south-west of Western Australia. The clone is estimated to be about 6400 years old but was only recently discovered. Prior to its discovery, part of the population was destroyed during the construction of a road. More recently the health of the population has declined and is threatened by a stem canker pathogen. This paper discusses the use of coppice treatment as a method of combating canker disease and restoring the health and vigour of the ramets within the population.

Keywords: *Eucalyptus phylacis*, meelup mallee, rare plant, clonal eucalypt, coppice

Introduction

Eucalyptus phylacis L.A.S.Johnson & K.D.Hill is a small mallee or tree up to 5 m tall, with distinctive rough and flaky bark on the stems, and produces creamy white flowers in February and March. It is commonly known as the Meelup mallee. It was only recently discovered and described (Hill and Johnson 1992) and survives as a single population in the Meelup Regional Park approximately 200 km south of Perth, Western Australia (Kelly *et al.* 1995). RAPD analysis showed that the population is made up of a single clone (Rossetto *et al.* 1999) comprising 27 known ramets (an individual plant derived from a clone) within an area of 0.09 ha. Based on the total area that the ramets occupy and assuming a peripheral growth rate of 0.5 cm year^{-1}, Rossetto *et al.* (1999) estimated the clone to be about 6400 years old, suggesting that it is potentially the oldest eucalypt plant on record. *E. phylacis* is thought to be a hybrid as it does not produce viable seed, despite producing masses of flowers annually and forming fruit. It grows on a loamy lateritic ridge near the coast in woodland dominated by *E. marginata* and *Corymbia calliphylla*. It is also within the geographic range of another closely related mallee, *E. decipiens*.

E. phylacis was originally discovered in 1981 by N. Marchant from the Western Australain Herbarium and the original collection made by K.H. Rechinger in 1982. It was declared as Rare Flora in 1987 under the *Wildlife Conservation Act* 1950 and ranked as Critically Endangered in 2003. The main threats to it are poor genetic diversity, poor regeneration, insect and fungal threats, modified fire regimes and road maintenance activities (Patten *et al.* 2004). Originally the population was larger, but prior to its discovery road construction (pre 1955), subsequent realignment and the development of a scenic lookout (between 1955 and 1966) destroyed an unknown number of ramets. Once the significance of the plant became known, access to the lookout was restricted and in 2002 a new lookout was constructed and the original site rehabilitated. In the early 1990s, damage by wood boring insects and canker development in the bark was observed on many stems. A number of canker-causing fungi, including *Botrysphaeria australis*, have recently been isolated and identified (Scott 2003). A large number of stems within the population have died and bark splitting (Fig.1a) and severe canker development (Fig. 1b,c) is evident on almost all the remaining stems. Meanwhile, an Interim Recovery Plan has been completed (Patten *et al.* 2004) that describes other management options that are being explored to aid the recovery and to promote the health of the population.

One practical option available for the recovery of *E. phylacis* is to coppice the ramets in order to promote new vigorous healthy growth. It is well known that mallee eucalypts re-sprout following fire (Noble *et al.* 1980, Noble 2001) and following removal of the stems by cutting (Noble 1982). Both events result in the rapid development of a multi stemmed habit arising from a woody rootstock or lignotuber (Noble 2001). It is also recognised that healthy vigorous plants are more resistant to pathogen attack and that canker diseases are more common in stressed and ageing individuals (Old and Davison 2000). Local records and knowledge suggest that the *E. phylacis* population has not experienced fire for 16 or more years. In contrast, many mallee environments are burnt regularly and mallee populations can regenerate freely from single fires every 5–10 years (Noble 1989). Therefore we suggest that the plants within the population are ageing, losing their vigour and are thus more prone to canker disease. In order to investigate whether *E. phylacis* will regenerate following fire or stem removal one of the 27 individual ramets was selected for mechanical coppice treatment. The results are reported here.

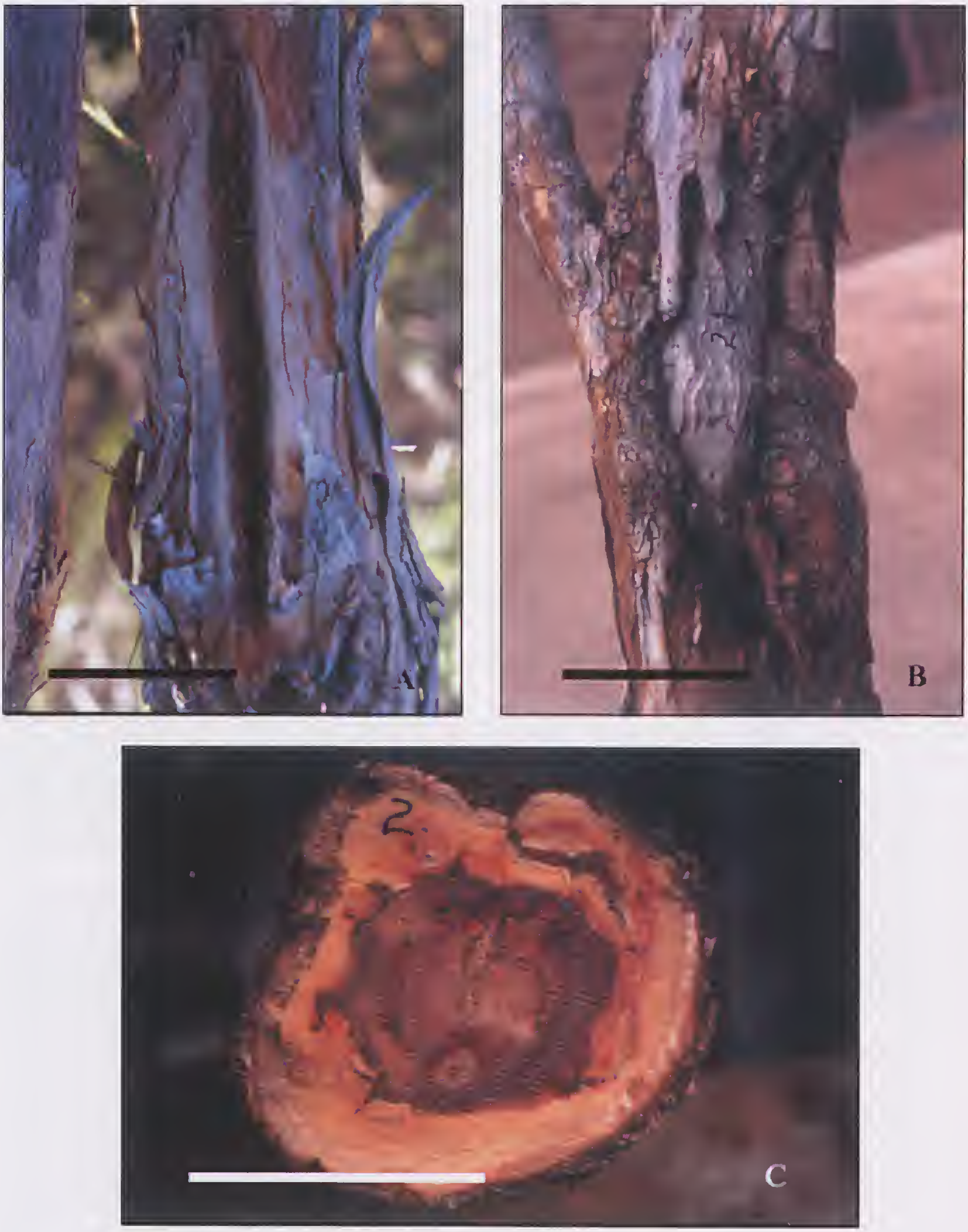

Figure 1. Canker damage common on stems of *E. phylacis*. A, superficial split in bark (bar = 5 cm); B, severe canker (bar = 5 cm); C, cross section of stem in Fig. 2b showing decay and discolouration of wood (bar = 5 cm).

Table 1

Attributes of stems removed from a coppiced *E. phylacis* ramet.

Stem #	Diameter (mm) at: Base	Diameter (mm) at: 1.3 m	Bark thickness (mm) at: Base	Bark thickness (mm) at: 1.3 m	Age (years)
1	98	66	–	–	Dead
2	171.5	103.5	15.5	15	20
3	102	71	16	11	16
4	75.5	58	13	9.5	13
5	85	53.8	12	9	20
6	62	54.5	–	–	Dead
7	185	137	15	15.5	20

Methods

Coppice treatment

In June 2001, a single ramet of *E. phylacis* was selected (on the basis of it being the one most severely affected by bark cankers) for coppice treatment. This involved severing all the stems at 25 mm above the lignotuber with a chainsaw. The selected ramet had seven stems, two of which were dead and five were severely affected by canker. All equipment was sterilised, and Steri-Prune wound sealant (Balchan International, Mulgrave, NSW), a bitumen-based product, was applied to the surface of all cut stems. Sections, 30 mm thick, were cut from the base of each stem and used to estimate the age of each stem by ring counts and to measure bark thickness. The remainder of the removed material was taken away and burnt and the ash then returned to the site and spread around the stump. The stump was protected from browsing animals with a wire cage.

Fire history

The date of the last fire was estimated using local Shire records, site inspection, aerial photos and the estimated ages of the removed *E. phylacis* stems. Each ramet was also inspected for signs of past fire damage in the form of burnt stem stumps and evidence of charcoal on the bark at the base of existing stems. *Hakea trifurcata* was the dominant shrub species present, and three *H. trifurcata* stems from within or immediately adjacent to the *E. phylacis* population were also removed and their ages estimated by ring counts. *H. trifurcata* is a species that regenerates from seed following fire, and their age is likely to indicate the time of the last fire. Ring counts were obtained using air-dried discs cut from the base of each stem. The surface of each disc was smoothed with a plane and sandpaper and two diameters were pencilled at right angles on each surface. Rings were counted visually or with assistance of a stereomicroscope using 6x or 10x magnification (Mucha 1979). Moistening the surface with water also made the rings appear clearer.

Table 2

Diameter (at 25mm above ground) and height of new coppice growth 24 months after cutting treatment to a ramet of *E. phylacis*.

Stem	Diameter (mm)	Height (cm)
1	10	110
2	45	250
3	40	230
4	30	250
5	20	180
6	45	230
7	40	210

Results

Stem age and bark thickness of *E. phylacis*

The estimated ages of the removed stems ranged from 13–20 years with diameters at breast height from 55–185 mm. The rhytidome (outer bark) was thin and flaky, about 1–2 mm thick, while the living inner bark was quite thick, ranging from 10–14 mm at the base and 6–14 mm at 1.3m height (Table 1).

Fire

Shire records indicate that a wildfire occurred immediately adjacent to and down slope from the *E. phylacis* population in 1985, 16 years previous to the study. Evidence of charcoal and burnt stem stumps on 70% of the *E. phylacis* ramets and standing dead stems with fire scars present on both *E. phylacis* and *C. calophylla* suggest that the 1985 fire entered the population and burnt the majority of the ramets. Ring counts estimated that the ages of the removed *H. trifurcata* plants were 12, 12 and 14 years. Comparing aerial photos from 1980 and 1992 did not show conclusive evidence or the boundary of the fire reported in 1985.

Coppice development

Three months after treatment, four new shoots were emerging from two of the stumps of main stems. Two months later, the resulting coppice had grown to about 30 cm in height (Fig. 2a). Fifteen months after treatment the coppice from the lignotuber was about 2 m tall and consisted of 10 vigorous stems (Fig. 2b) and 24 months after treatment 6 stems, 20–45 mm in diameter, had grown to 3 m or more in height and dominated the development (Table 2, Fig. 2c). Four of the stumps from the original stems produced new coppice while two stems of the new coppice arose from the surface of the lignotuber.

Discussion

Clonal development in lignotuber-forming mallee eucalypts appears to be more common in situations that

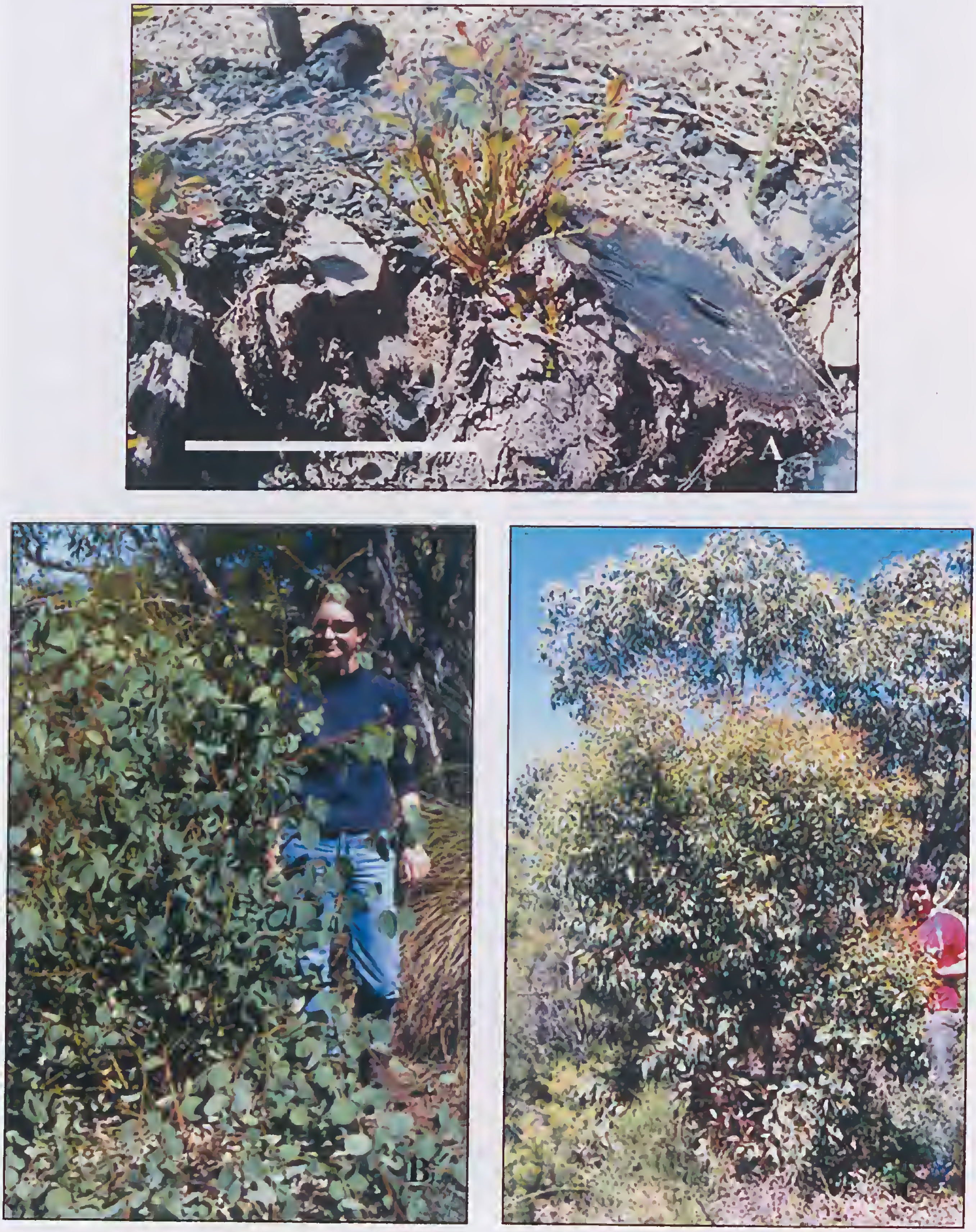

Figure 2. Shoot and coppice development following removal of stems from an *E. phylacis* ramet. A, shoot development 5 months after treatment (bar = 15 cm); B, coppice development (about 1.8 m tall) with juvenile foliage 15 months after treatment; C, coppice development (about 3.2 m tall) with adult foliage 24 months after treatment. The mature ramet in the background is approximately 4.5 m tall.

favour lateral growth such as sites with high light availability, limited soil nutrients and frequent fire (Noble 1982). Observation of the surrounding landscape suggests that the area has not been burnt for many years. The presence of burnt stem stumps and burnt dead stems along with the ring counts of the removed *E. phylacis* stems suggests that a fire may have burnt at least part of the mallee population 16 years previously. The main population is quite fragmented due to past road construction and is split into four distinct groups. The group in which the coppiced ramet exists was likely to have been exposed to the fire, but the other groups have the protection of a wide cleared gravel area between them and the shrub-covered slope below. The larger stem diameters of the 'protected' ramets (Scott 2003) also suggests that they are older and probably escaped being burnt or if they were burnt their stems were not killed. The thick bark on *E. phylacis* stems (Table 1) suggests that they could survive a fire of moderate intensity (Vines 1968). The ring counts of the *H. trifurcata* shrubs also indicate that the 1985 fire burnt the slope directly below the mallee population.

After a canopy killing fire, mature mallee plants re-sprout from a large lignotuber (Noble 1982, Gill 1997), and within Australia's mallee region, many eucalypts are maintained in a youthful form either through regular burning and/or edaphic factors (Beadle 1968, Noble 1982). It has been suggested that fire can be managed for the benefit of some mallee communities and, for mallee communities in the arid region of southern Australia, Noble (1982) suggested a fire interval of about 10 years. In lieu of fire, however, mallee eucalypts will re-sprout successfully following removal of stems by cutting, both in the spring or the autumn (Noble 1982). Two years following coppice treatment, the *E. phylacis* ramet had attained a height of more than 2 m with 6 dominant stems. Noble (1982, 2001), however, also showed that autumn burning or coppice treatment two years in a row killed mallee eucalypts, but the same treatment in spring resulted in few tree deaths.

In natural environments, it is generally accepted that high incidence and severity of cankers are associated with environmental stress (Old and Davison 2000) or alternatively low tree vigour, which is common in older, over-mature plants. Generally, vigorous healthy trees are more resistant to attack from both insect pests and fungal pathogens. In the case of the *E. phylacis* population, we hypothesised that the individual ramets are over-mature and that their vigour will be reinstated by promoting new, healthy growth either by burning or by stem removal by cutting which will promote coppice development. Future monitoring will determine whether the coppice will be resistant to infection and canker development, but after 2 years all stems are canker free.

While tissue culture may secure the future of rare eucalypts, including *E. phylacis* (Bunn 2001) it will not save the individual ramets in the population at Meelup. The future of the present *E. phylacis* population depends on rejuvenating the health of the stand. It would appear that fire might be an appropriate tool, as has possibility been the case for the past six millennia, and intervals of 10–15 years may keep the population physically viable and with sufficient vigour to resist fungal pathogens.

However, because of the location of the site and the situation of the species it may not be practical or wise. For example, other factors such as the fire interval required for reproduction in other associated species in the habitat, and the proximity of the population to urban and other public areas also needs to be considered. The greatest threats to restricted species such as *E. phylacis* are catastrophic events or further disturbance that will lead to extinction (Rossetto *et al.* 1999). Burning the entire population in a single fire event may not, therefore, be desirable, and if burnt it may need to be protected from repeated fire for several years in order to ensure complete regeneration. But the fragmented nature of the population does provide a possibility of reducing the risk associated with burning the entire population.

An alternative that we propose is a program of gradual coppice treatment to be initiated, where one or two ramets are coppiced in the spring every 1–3 years. A 10–15 year program will result in the rejuvenation and ensure the future of the entire population. Because of the Critically Endangered and Declared Rare status of *E. phylacis*, only one ramet was selected for treatment, but it was the one considered as having the most advanced symptoms of infection and senescence. The result shows promise for the other ramets within the population. When the health and vigour of the entire population is restored, it is feasible that some of the major environmental threats to the species will be abated and future management of the population could be integrated into the overall management of the reserve, which may include fire. If managed successfully, *E. phylacis* will always be rare, but need not be endangered.

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Seedling growth and physiological responses of two sandplain *Banksia* species differing in flood tolerance

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Abstract

Banksia littoralis (Proteaceae) inhabits winter-wet locations and wetland fringes that are prone to seasonal flooding events on the Swan Coastal Plain. To survive in these locations, *B. littoralis* seedlings must be able to tolerate periods of flooding or complete submergence if establishment is to be successful. Flood tolerance was assessed in seedlings of *B. littoralis* subjected to 104 days of continual soil waterlogging by comparing changes in seedling growth and leaf ecophysiology with those of well-watered plants. Flood tolerance was also assessed in seedlings of *Banksia prionotes*, a species that grows in drier locations on the Swan Coastal Plain. As expected, *B. prionotes* was unable to survive long periods of soil waterlogging or submergence (97% mortality after 72 days of flooding). Both species responded to flooding by closing their stomates and reducing photosynthetic capacity, although *B. littoralis* was able to recover lost photosynthetic potential when flooded conditions subsided. After 72 days of flooding, there was a substantial decrease in relative growth rate in flooded *B. prionotes* seedlings, compared to that of well-watered plants, although this was not associated with significant differences in biomass allocation. Flood-affected *B. littoralis* seedlings were significantly smaller than well-watered seedlings after 72 days of flooding, but were the same size after 104 days. Flood tolerance enables *B. littoralis* seedlings to survive exceptionally wet winter-spring months when flooding events are more likely to occur, although surviving the annual summer drought may be more important to sustain seedling establishment.

Keywords: *Banksia littoralis*, *Banksia prionotes*, flooding, photosynthetic capacity, stomatal conductance, submergence

Introduction

Species confined to wetland fringes and winter-wet depressions are being lost from Perth's Swan Coastal Plain as a result of declining groundwater levels and poor groundwater recharge, due to local and regional abstraction, and successive years of below average rainfall (Aplin 1976; Groom *et al.* 2000, 2001). The loss of Swamp Banksia (*Banksia littoralis* R.Br.; Proteaceae) trees and its replacement by more xeric *Banksia* species has occurred over the past 40 years (Groom *et al.* 2001) as winter-wet swamps become filled with sand from the surrounding dunes (Heddle 1980; Muir 1983). This may have been because *B. littoralis* trees were unable to access sufficient moisture to meet their summer water-use requirements as soil moisture content and groundwater levels declined (Groom *et al.* 2001; Groom 2002; Zencich 2003).

Decreasing occurrence of flooding events may be an alternative explanation for the loss of tree species from wetland fringes, as it directly impacts seedling recruitment and establishment. Flooding is not necessarily required to sustain the recruitment and survival of wetland tree seedlings (Froend *et al.* 1993) but may provide sufficient soil moisture for seedlings to survive post-winter and subsequent dry summers. During flooding events, seedlings of wetland species must either be flood-tolerant or tolerate periods of submergence if seedling establishment is to be successful. The ability of seedlings to tolerate flooding or submergence may be an important contributor to a species' ecological distribution.

This paper compares the seedling flood response strategies of *Banksia littoralis*, a tree species known to tolerate flooding events, and a congener from the Swan Coastal Plain that typically grows in drier locations (*B. prionotes* Lindl.) (Groom 2004). Differences in flood responses and ability to tolerate complete submergence are measured in terms of changes in growth and leaf ecophysiology.

Methods

Setup and Design

Banksia seeds were obtained from Nindethana Seed Supply (Albany, WA). Seeds were imbibed in tap water for 30 min before being placed in plastic petri dishes lined with moist filter paper, and germinated at 15°C, the optimal germination temperature for other southwest

Australian *Banksia* species (Cowling & Lamont 1987). Once germinated, seeds were transferred to shallow seedling trays containing washed, coarse white sand in a temperature controlled glasshouse. In January 2001, 80 seedlings per species were transferred into square pots 18 cm tall by 8 cm wide, each containing coarse white sand with a top layer of small stones. Flooding trials began on 27 April 2001 and concluded 104 days later.

Flooding was achieved using three 60 L clear plastic tubs each containing 10 pots per species. Tubs were filled with tap water until the pot, but not the seedling, was completely emersed. Another three tubs, set up exactly the same except with drainage holes, were watered twice a week for the duration of the flooding trial, and used as controls. Every two weeks seedlings were removed and all the tubs drained and scrubbed with tap water to remove the build up of algae on the tub walls. Seedlings were then put back into the tubs and refilled with fresh tap water. Four seedlings per species were removed from the tubs to assess the species' ability to recover after 36 days of flooding.

To examine the effects of submergence, 5–10 seedlings per species were placed in a 90 L clear plastic tub. This was filled with tap water until all plants were completely submerged. This tub was cleaned and refilled with fresh tap water every two weeks. Physiological data (stomatal conductance, chlorophyll fluorescence) were not collected from submerged plants because the leaves were constantly under water.

Stomatal conductance

Stomatal conductance and chlorophyll fluorescence data were measured approximately every 2 weeks from 4 plants per species and treatment. Midday stomatal conductance (g_s) was measured on recently formed, fully-expanded leaves using a portable infra-red gas analyser (LCi, ADC Bioscientific Ltd, Hoddesdon, England) attached to a leaf chamber. Measurements were taken on relatively cloud-free, sunny days, with data collected within 1 min of enclosing the leaf. Conductance data were collected at ambient humidity and CO_2 concentrations and when light intensity (PAR) was greater than 1000 µmol m^{-2} s^{-1}. Day time air temperature within the glasshouse varied from 23–25°C.

Chlorophyll fluorescence

Chlorophyll fluorescence was measured on attached leaves using a modulated chlorophyll fluorometer (OS1-FL, Opti-Sciences, Tyngsboro, Massachusetts, USA). Midday measurements of potential photochemical efficiency of Photosystem II (F_v/F_m) were recorded after a leaf dark adaptation time of 30 min using leaf clips provided by the fluorometer manufacturer. A reduction in the F_v/F_m ratio commonly indicates the occurrence of photoinhibition, particularly in plants exposed to periods of stress (Maxwell & Johnson 2000). Measurements were recorded from 4 plants per species and treatment.

Actual efficiency of Photosystem II photochemistry, or quantum yield (Φ_{PSII}), was measured under natural light conditions on light-exposed leaves, using an additional light pulse during the midday period. Φ_{PSII} was calculated by the instrument according to Genty *et al.* (1989). Φ_{PSII} was collected at PAR light intensity > 1000 µmol m^{-2} s^{-1} and is used as an indication of overall photosynthetic performance (Maxwell & Johnson 2000).

Seedling growth

Four seedlings per species and treatment were harvested at the beginning of the experiment (27 April 2001), towards the end (4 July) and at the end (7 August, *B. littoralis* only). Each seedling was separated into leaf, shoot (stem and side branches) and root components and

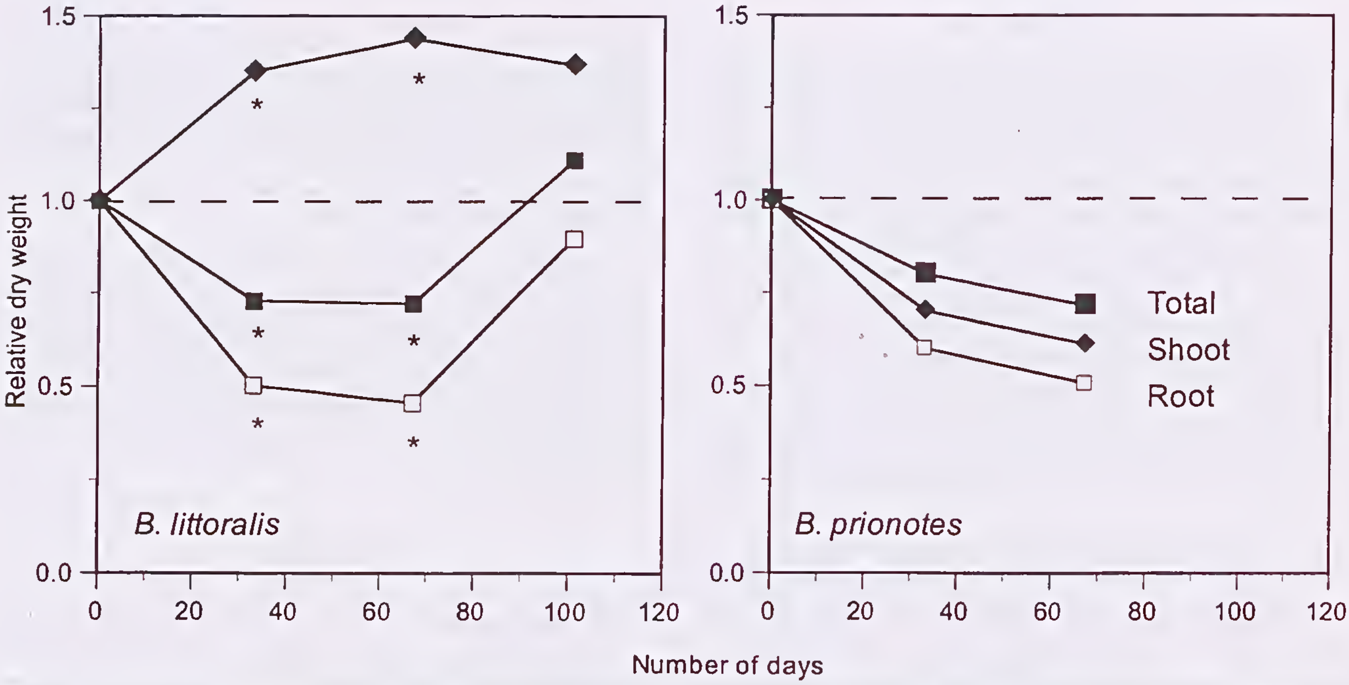

Figure 1. Relative total (closed square), shoot (diamond) and root (open square) dry weight of *Banksia* seedlings subjected to continuous flooding. Data are means of four replicates and relative to data obtained for well-watered (control) seedlings. Dashed line (at 1) indicates where flood and control data would be equal. Asterisk indicates significant differences ($P<0.05$) between flooded and well-watered seedlings. SE bars are not included because of their overlapping nature.

Table 1

Growth parameters of *Banksia littoralis* seedlings before and after an exposure to an extended flooding regime. Values are mean ± SD for 4 plants. % change indicates an increase (+) or decrease (-) in relation to the pre-flooding data. *P* values based on a *t*-test comparing well-watered and flooded data. RGR = relative growth rate; LAR = Leaf area ratio.

		72 days of flooding			% change	
	Before Flooding	Well-watered	Flooded	*P*	Well-watered	Flooded
Dry weight (g)						
Total	0.66 ± 0.06	1.80 ± 0.36	1.30 ± 0.19	0.0415	+173	+97
Shoot	0.24 ± 0.03	0.49 ± 0.11	0.70 ± 0.13	0.0465	+104	+192
Roots	0.42 ± 0.06	1.31 ± 0.28	0.60 ± 0.16	0.0042	+212	+43
Root:shoot ratio	1.80 ± 0.29	2.75 ± 0.52	0.88 ± 0.31	0.0009	+53	-51
RGR – total (mg g^{-1} day^{-1})		13.9	9.4			
RGR – shoot (mg g^{-1} day^{-1})		23.6	12.7			
LAR (mm^2/mg shoot)	5.60 ± 0.42	4.46 ± 0.23	3.48 ± 0.52	0.0143	-20	+39
Seedling height (cm)	10.6 ± 2.1	14.6 ± 3.8	14.8 ± 3.2	0.7979	+38	+39
		104 days of flooding				
Dry weight (g)						
Total		1.70 ± 0.44	1.89 ± 0.80	0.8103	+158	+186
Leaves & shoots		0.77 ± 0.28	1.06 ± 0.40	0.2939	+221	+342
Roots		0.93 ± 0.27	0.84 ± 0.54	0.5373	+121	+100
Root:shoot ratio		1.30 ± 0.52	0.80 ± 0.40	0.1754	-28	-55
RGR – total (mg g^{-1} day^{-1})		9.1	10.1			
RGR – shoot (mg g^{-1} day^{-1})		11.2	14.3			
LAR (mm^2/mg shoot)		3.79 ± 0.55	3.17 ± 0.28	0.0918	-32	-43
Seedling height (cm)		13.6 ± 3.6	13.9 ± 2.5	0.8253	+28	+31

their weight recorded after drying for 24 h at 60°C. Leaf area was measured on fresh samples using a digital image analyser (WinDIAS, Delta-T Devices, Cambridge, UK). Stem lengths were also recorded. Relative growth rates (RGR) were calculated on a shoot and total dry biomass basis as described by McGraw and Garbutt (1990).

Results

Banksia littoralis

After 72 days of flooding, flooded *B. littoralis* seedlings were significantly smaller (total dry weight) than the well-watered seedlings, with more dry mass allocated to their stem and leaves, but less leaf area per shoot weight (Table 1). The root:shoot ratios of well-watered seedlings were 53% greater than pre-flood seedlings, in contrast to flooded seedlings where root:shoot ratios were 51% lower. Overall shoot mass of flooded seedlings was significantly greater than that of the well-watered controls (Fig 1) whereas root mass was significantly lower. There was no significant difference between flooded and well-watered seedlings in any of the growth parameters measured after 104 days of flooding (Table 1). Well-watered seedlings had a greater relative growth rate than flooded seedlings after 72 days, in contrast to relative growth rate after 104 days. There was no seedling mortality during the 104 days of flooding.

There were significant declines in g_s, Φ_{PSII} and F_v/F_m

Table 2

Stomatal conductance (g_s), maximum (F_v/F_m) and actual quantum yield (Φ_{PSII}) of Photosystem II photochemistry of *Banksia littoralis* seedlings before and after exposure to an extended flooding regime. Values are mean ± SD for 4 plants. % change indicates an increase (+) or decrease (-) in relation to the well-watered data. *P* values based on a *t*-test comparing well-watered and flooded data.

		17 days of flooding			
	Before Flooding	Well-watered	Flooded	*P*	% change
g_s (mol m^{-2} s^{-1})	0.19 ± 0.07	0.25 ± 0.02	0.11 ± 0.04	0.0407	-56
Φ_{PSII}	0.43 ± 0.12	0.44 ± 0.03	0.19 ± 0.04	0.0008	-57
F_v/F_m	0.84 ± 0.02	0.82 ± 0.02	0.68 ± 0.09	0.0299	-17
		74 days after flooding			
g_s (mol m^{-2} s^{-1})		0.18 ± 0.06	0.07 ± 0.02	0.0164	-61
Φ_{PSII}		0.44 ± 0.06	0.32 ± 0.05	0.1230	-28
F_v/F_m		0.86 ± 0.02	0.76 ± 0.08	0.0454	-12

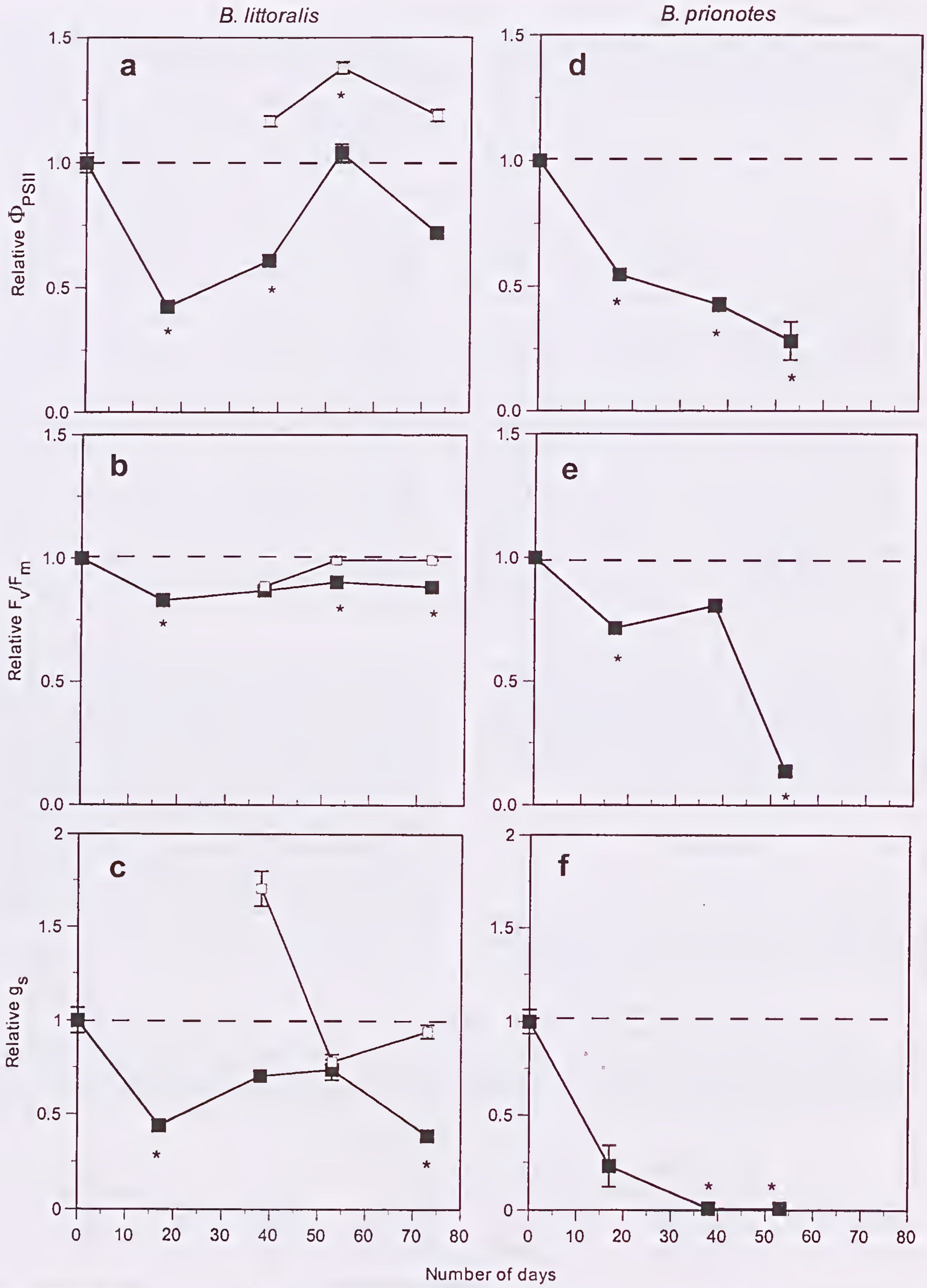

Figure 2. Relative fluorescence (Φ_{PSII}, F_v/F_m) and stomatal conductance (g_s) of *Banksia littoralis* (a–c) and *B. prionotes* (d–f) seedlings subjected to continuous flooding. Closed squares represent flooded seedlings, open squares (*B. littoralis* only) represents seedlings removed from the flooding process and allowed to recover. Data are mean ± SE for four replicates and are relative to data obtained for well-watered (control) seedlings. Dashed line (at 1) indicates where flood and control data would be equal. Asterisk indicates significant differences ($P<0.05$) between flooded affected and well-watered seedlings.

Table 3

Growth parameters of *Banksia prionotes* seedlings before and after an exposure to an extended flooding regime. Values are mean ± SD for 4 plants, including some recently dead plants. See Table 1 for details on statistics and abbreviations.

		72 days of flooding			% change	
	Before Flooding	Well-watered	Flooded	P	Well-watered	Flooded
Dry weight (g)						
Total	0.53 ± 0.14	1.14 ± 0.51	0.70 ± 0.17	0.1604	+115	+32
Shoot	0.34 ± 0.10	0.57 ± 0.26	0.41 ± 0.12	0.3735	+68	+21
Roots	0.22 ± 0.064	0.57 ± 0.25	0.30 ± 0.08	0.6370	+159	+36
Root:shoot ratio	0.57 ± 0.14	1.01 ± 0.12	0.72 ± 0.22	0.0791	+77	+22
RGR – total (mg g^{-1} day^{-1})		10.6	3.9			
RGR – Shoot (mg g^{-1} day^{-1})		7.2	2.6			
LAR (mm^2/mg shoot)	5.37 ± 0.89	6.22 ± 1.37	3.61 ± 0.51	0.0205	+16	-33
Seedling height (cm)	0.9 ± 0.4	1.6 ± 0.8	0.8 ± 0.3	0.0323	+78	-11

resulting from flooding on the 17th day (Table 2), resulting in 17% to 56% decreases in relation to pre-flood values. After 74 days of flooding, all three variables were less than those of well-watered seedlings (Fig. 2), although there was no significant different in Φ_{PSII} between well-watered and flooded seedlings (Table 2). Stomatal responses were overall linearly positively correlated with Φ_{PSII} ($r = 0.65$, $P < 0.05$), with *B. littoralis* possessing a higher g_s at a given Φ_{PSII} than *B. prionotes.*

There was no significant difference in the physiology of seedlings after 8 days recovery from flooding compared with well-watered seedlings (Fig 2 a–c). This was despite Φ_{PSII} and g_s displaying greater values than the well-watered controls. Φ_{PSII} was the only parameter to show significant differences after 18 days of recovery ($P = 0.0454$). There was no significant physiological difference between recovered and control plants after 38 days of recovery (Fig 2 a–c).

Banksia prionotes

After 28 days of flooding 22% of *B. prionotes* seedlings had died. An additional 14 seedlings died 4 days later taking the cumulative mortality to 45%. After 53 days of flooding seedling mortality was 83%. The experiment was concluded after 72 days, with only two of the original 60 seedlings still alive. All seedlings used to monitor post-flooding recovery died after 8 days.

After 72 days of flooding the percentage difference in dry weight increased by 21 to 36% (Table 3) compared to pre-flood values, and was less than that for control plants (68 to 159%). This difference between flooded and well-watered plants is reflected by the relative growth rate values over the same time period. There was no significant difference in total dry weights, the weights of the stem and roots, or root:shoot ratios (Table 3) between well-watered and flooded after 72 days of flooding. Despite this, well-watered seedlings were significantly taller ($P = 0.0323$), and produced more leaf area per shoot dry weight. Throughout the period of flooding, total, shoot and root dry weights of flooded seedlings were consistently less than that of the well-watered seedlings (Fig 1), but there was no significant difference between the two treatments.

After 17 days of flooding there was a significant decline in stomatal conductance (g_s), compared with that of pre-flooded seedlings ($P = 0.0097$). This was despite no significant difference in g_s between well-watered and flooded treatments measured on the 17th day, attributed to the larger standard deviation of well-watered seedlings. After 38 days of flooding g_s was <0.01 mol m^{-2} s^{-1} and remained so when remeasured after 54 days (Fig 2).

There was a significant decline in actual (Φ_{PSII}) and maximum (F_v/F_m) efficiency of photosystem II

Table 4

Stomatal conductance (g_s), maximum (F_v/F_m) and actual quantum yield (Φ_{PSII}) of Photosystem II photochemistry of *Banksia prionotes* seedlings before and after exposure to an extended flooding regime. See Table 2 for details.

		17 days of flooding			
	Before Flooding	Well-watered	Flooded	P	% change
g_s (mol m^{-2} s^{-1})	0.14 ± 0.05	0.13 ± 0.11	0.04 ± 0.01	0.2765	-69
Φ_{PSII}	0.41 ± 0.05	0.43 ± 0.02	0.24 ± 0.09	0.0312	-44
F_v/F_m	0.80 ± 0.04	0.84 ± 0.02	0.60 ± 0.15	0.0222	-29
		54 days after flooding		P	
g_s (mol m^{-2} s^{-1})		0.12 ± 0.06	<0.01	-	-
Φ_{PSII}		0.54 ± 0.06	0.15 ± 0.11	0.0044	-72
F_v/F_m		0.84 ± 0.01	0.11 ± 0.08	0.0001	-87

Table 5

Shoot and root dry weights of *Banksia prionotes* and *B. littoralis* seedlings after 54 days of total submergence in comparison to well-watered seedlings. Values are mean ± SD for 4 plants. % change indicates an increase (+) or decrease (-) in relation to pre-flood data. *P* values based on a *t*-test comparing well-watered and submerged data.

	54 days of submergence			% change
	Well-watered	Submerged	*P*	Submerged
B. prionotes				
Dry weight (g)				
Total	1.14 ± 0.51	0.33 ± 0.08	0.0070	-38
Shoot	0.57 ± 0.26	0.18 ± 0.08	0.0166	-47
Root	0.57 ± 0.25	0.16 ± 0.02	0.0038	-27
Root:shoot ratio	1.01 ± 0.12	1.1 ± 0.63	0.7774	+93
RGR - total (mg g^{-1} day^{-1})	14.5	-8.7		
RGR - shoot (mg g^{-1} day^{-1})	9.7	-12.5		
B. littoralis				
Dry weight (g)				
Total	1.80 ± 0.36	1.02 ± 0.23	0.0236	+54
Shoot	0.49 ± 0.11	0.37 ± 0.07	0.1801	+35
Root	1.31 ± 0.28	0.65 ± 0.25	0.0227	+55
Root:shoot ratio	2.75 ± 0.55	1.83 ± 0.90	0.1483	+2
RGR – total (mg g^{-1} day^{-1})	18.9	8.2		
RGR – shoot (mg g^{-1} day^{-1})	13.5	8.4		

photochemistry after 17 days of flooding compared with that of pre-flooded seedlings (Fig 2), and a significant difference when compared with well-watered seedlings (Table 4). As flooding continued, there was a significant decrease in both fluorescence parameters, resulting in a -72 to -87% change after 54 days. A decrease in Φ_{PSII} was associated with decreased stomatal conductance, as the two variables were positively linearly correlated ($r = 0.88$, $P < 0.01$).

Submergence

All submerged *B. littoralis* seedlings survived after 54 days, although many of the existing leaves were a lighter green compared to controls. Φ_{PSII} measurements taken on the 17th day were not significantly different ($P = 0.3500$) between well-watered (0.44 ± 0.03) and submerged seedlings (0.32 ± 0.20). Submerged plants had significantly lower total and root dry weight than well-watered plants, but not shoot dry weight (Table 5), with a 54% increase in total dry weight in relation to pre-flood seedlings. There was no significant difference in root:shoot ratios between the control and submerged plants.

All *B. prionotes* seedlings died after 54 days of submergence. Φ_{PSII} measurements taken on the 17th day showed a significant difference ($P = 0.0050$) between well-watered (0.41 ± 0.03) and submerged seedlings (0.21 ± 0.05). Submerged plants had significantly lower dry weight than well-watered plants (Table 5), with a 38% reduction in total dry weight in relation to pre-flood seedlings, represented by negative RGR values. There was no significant difference in root:shoot ratios between controls and submerged plants.

Discussion

Mortality, physiology and growth data support the hypothesis that *B. littoralis* seedlings are more flood tolerant than *B. prionotes* seedlings. *Banksia prionotes* was unable to survive long periods (> 70 days) of flooding, and displayed many of the physiological and morphological responses typical of flood-intolerant species. These include stomatal closure, which has been associated with a decrease in root hydraulic conductivity (Davies & Flore 1986; Else *et al.* 2001), a decline in photosynthetic capacity, reduced growth and increased mortality. *Banksia littoralis* also displayed a reduction in stomatal conductance and photosynthetic performance (Φ_{PSII}) in response to flooding, but not to the same extent as *B. prionotes* and, like most flood tolerant species, was able to resume photosynthesis after the flooding treatment ceased.

There is evidence to suggest that a decrease in stomatal opening and its limitation on CO_2 intake, followed by a decrease in total leaf area, are the main factors contributing to reduced carbon uptake and reduced whole plant biomass in flooded seedlings (Smith & Moss 1998; Mielke *et al.* 2003). This is partially supported by this study, except that photosynthetic processes were directly affected by damage sustained to photochemical reaction centres (as indicated by a reduction in F_v/F_m and Φ_{PSII} ratios). Despite this reduction in photosynthetic performance, *B. littoralis* was able to maintain levels of Φ_{PSII} that were > 50% of that in well-watered plants, resulting in an increase in biomass that was 97% greater than pre-flood plants after 72 days of flooding. For flooded *B. prionotes* seedlings a reduction in relative growth rate can be directly linked to a reduction in photosynthetic activity, despite the lack of significant differences in biomass allocation.

The higher rate of *B. prionotes* mortality may be closely linked to the roots inability to survive and function under oxygen-deficient conditions. This caused severe physiological dysfunction, resulting in a progressive decline in photosynthetic performance. For *B. littoralis* seedlings to survive more than 100 days of flooding implies adaptations that promote oxygen and nutrient uptake. This may include the formation of aerenchyma tissues or presence of hypertrophied lenticels (Kozlowski 1997), although these were not examined.

Although flood survival is important for *B. littoralis* seedlings, flooding events are episodic in nature and restricted to winter and spring months. Surviving the annual summer drought may be more important for seedling recruitment. Physiological data suggests that *B. littoralis* is inherently less water-use efficient (assuming $\Phi_{PSII}/g_s \approx$ photosynthesis/water transpired) than xeric congeners, and is similar to results obtained for *B. littoralis* under drought conditions (Groom 2002). Seedlings of *Banksia littoralis* can be classified as 'water spenders' in response to flooding (this paper) and gradual summer drought (Groom 2002). By maintaining a relatively high rate of stomatal conductance (0.1–0.2 mol m^{-2} s^{-1}; 50–75% of well-watered plants) during flooding, *B. littoralis* was able to support sufficient photosynthetic activity to allow shoot growth to occur at a rate similar to, or greater than, well-watered plants. *Banksia littoralis* seedlings are able to maintain stomatal conductance between 0.2–0.3 mol m^{-2} s^{-1} until volumetric soil moisture contents drop below 2% (Groom 2002). For *B. littoralis* seedlings, an overall higher g_s as compared to more xeric congeners, may be viewed as a flood survival technique and/or a response to year-round access to reliable water sources.

The lack of post-flooding physiological recovery and the greater sensitivity of *B. prionotes* to waterlogging is not surprising considering this species characteristically occurs on well-drained, sandy soils (Taylor & Hopper 1988). *Banksia littoralis* inhabits winter-wet locations and wetland fringes, tolerating up to 104 days of water inundation (this study), without detrimental impacts on leaf ecophysiology once waterlogging ceased. This enables *B. littoralis* seedlings to survive exceptionally wet winter-spring months when flooding events are more likely to occur. *Banksia littoralis* seedlings also survived and sustained growth after being fully submerged for 54 days, although in this experiment the leaves tended to discolour and were prone to epiphytic algae growth. Although the impact of submergence on seedling recruitment in *B. littoralis* has yet to be quantified, species that grow well when waterlogged or grown in flood conditions are unlikely to do as well when subjected to extensive periods of submergence (Parolin 2001; Mauchamp & Méthy 2004).

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Notes on the geomorphology of The Humps, near Hyden, Western Australia

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Abstract

The domical inselberg or bornhardt known as The Humps is in many respects typical of the many granitic residuals of the Wheatbelt. Of great antiquity, it is a two-stage form which was initiated beneath a regolithic cover, and has been exposed in stages. Its minor forms (pitting, gnammas of various types, polygonal cracking, sheet structure) are also commonplace, though in some instances, such as the armchair-shaped hollows, they are especially well developed. But the evidence for its great age, for episodic exposure, and for the subsurface initiation of tafoni is noteworthy.

Keywords: bornhardt, multistage, tafoni, armchair-shaped hollow, mogote

Introduction

The Humps is a stepped bornhardt inselberg shaped in Late Archaean (2.55–2.75 Ga) granitic rocks and located some 20 km NNE of Hyden in the Western Gneiss Terrane of the Yilgarn Craton (Chin *et al.* 1984; Myers 1990). It stands more than 420 m above sea level and about 80 m above the surrounding plains (Fig 1). It displays several gross and minor features that are typical of other inselbergs in the region, and some that are peculiar to the site. For example, a perched block and plinth, an hourglass rock, split rocks and tafoni can be seen on the hill, which is characteristically bald and domical, but the evidence of great antiquity and of the subsurface initiation of tafoni are sufficiently rare to be noteworthy.

Origin of the bornhardt

The stepped morphology of The Humps (Figs 1 & 2) suggests that the residual was initiated in the subsurface and subsequently exposed as a result of periods of lowering of the surrounding plains, *i.e.* a two-stage or etch origin involving episodic exposure (Falconer 1911; Twidale 1964, 1982a, 1982b, 1982c; Twidale & Bourne 1975a). Such an interpretation implies differential subsurface weathering, and in particular the relative resistance to subsurface moisture attack of the compartment of rock that is The Humps. It might be argued that intrusive veins, which are particularly numerous on The Humps, as compared with, for example, King Rocks and Hyden Rock, have buttressed and strengthened the rock mass. First, however, the most common intrusions, namely pegmatites, are zones of weakness for they have been exploited to produce shallow linear depressions and steepened slopes (see also Bourne & Twidale 2002). Second, though density of intrusive sills and veins varies there is no reason to think that The Humps is more buttressed in this way than the immediately adjacent areas. To the contrary, in other areas such as the Pilbara, granite with numerous veins of aplite and quartz has been differentially weathered and eroded to produce an inselberg landscape, with veins exposed in both hill and plain.

The Humps, like other inselbergs in the vicinity, is massive. The few open fractures are widely spaced. A strong structural grain trending NW-SE or NNW-SSE (but locally variable) pervades the rocks of the Western Gneiss Terrane (*e.g.* Chin *et al.* 1984) and many of the more prominent outcrops (as indicated by their being named) occur in SE-NW corridors (Fig 3). Thus considering the Hyden area, Graham Rock, The Humps, Anderson Rocks and Mt Walker can be linked in this way, as can Gibb Rock, King Rocks, Bushfire Rock/Cockatoo Rock and a group of bornhardts in the Varley-Holt Rock district. Some of the bornhardts named also occur in roughly east-west (or ESE-WNW) alignments, as for instance Murray Rock, King Rocks, The Humps and Camel Peaks, and Cockatoo Rock/Bushfire Rock, Graham Rock, Hyden Rock, Captain Roe Rock/Mettam Knob and Karlgarin Hills. This suggests that the residuals may be preserved by virtue of compression associated with cross- or interference folding, first (and in terms of present orientations) NE-SW, and later roughly north-south; but whether as a result of direct compression or of shearing is not known, though persistent horizontal plate motions and evidence of conjugate *en echelon* fracture patterns favour the latter.

Episodic exposure and antiquity

As previously mentioned, the stepped morphology of The Humps (Figs 1 & 2) suggests episodic exposure. Four surfaces have been identified. Level I is of limited areal extent and is preserved in the highest crests. Level IV comprises the present plains and platforms (I *in* Fig 1). Level III takes the form of platforms preserved in spurs and perched some 30 m above present plain level. The most prominent planate surface remnants are referred to as Level II, 60–70 m above the surrounding plain. The

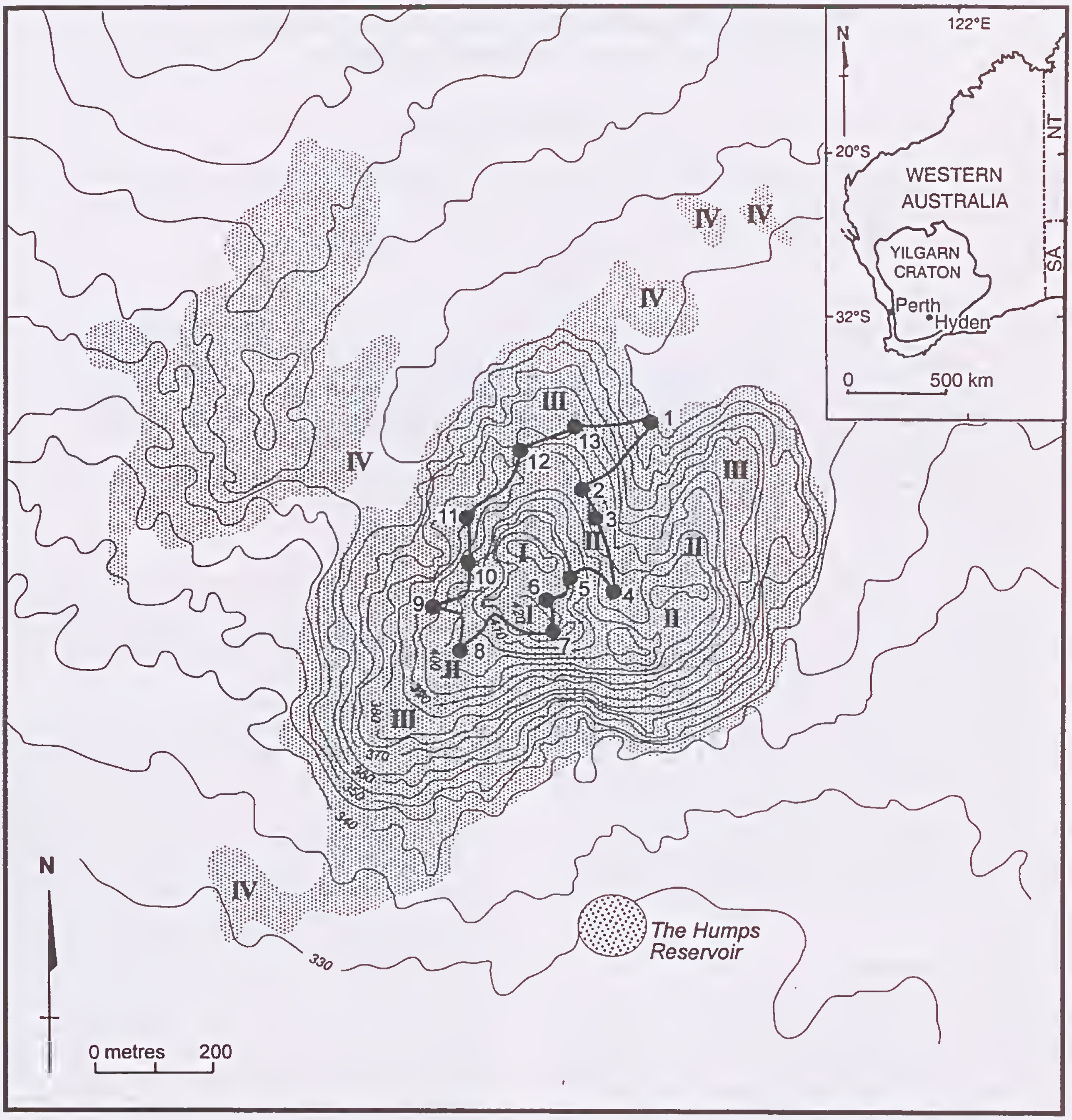


Figure 1. The Humps showing the outcrop (stippled), contours and levels I–IV. A suggested environmental walk, with thirteen sites exemplifying features of interest with reference to later Figures in this paper, viz. 1, platform (Fig 2); 2, joint clefts; 3, armchair-shaped hollow (Fig 8), pans and doughnuts; 4, flared slope, relic vegetation (Fig 6); 5, multiple flared slope (Fig 4); 6, joint cleft; 7, pans, pitting, boxwork, tramlines (Fig 9); 8, boulders on dome, polygonal cracking (Fig 11); 9, rock basins and buttressed slope (Fig 10); 10, sheet structure (Fig 7B); 11, boulders, tafoni, alveolar weathering, split rock, polygonal cracking; 12, boulders, perched, hourglass, split rock with tafone (Fig 12); 13, split boulder with window. Inset map of Western Australia showing location of Hyden. The Humps stands some 20 km NNE of the town of Hyden.

best developed flared slopes (Fig 4; 5 *in* Fig 1) are associated with this surface (Twidale 1962, 1968; Twidale & Bourne 1998a) as are large boulder fields which suggest prolonged and intense shallow subsurface weathering. Level II is readily correlated with the primary lateritic remnants of later Cretaceous age (Clarke 1994; Twidale & Bourne 1998b) preserved on adjacent plateaux and high plains (Fig 5). The pisolitic ironstone (or ferricrete: see Twidale 1976, pp. 196–197) exposed in shallow pits close to the northwestern base of the inselberg is interpreted as a secondary or derived deposit lacking the kaolinised mottled and pallid zones of a laterite profile. It accumulated in a scarp-foot depression which formed as a result of weathering and lowering by runoff from the hill and which is typical of inselberg landscapes (Thorbecke 1927; Clayton 1956; Dumanowski

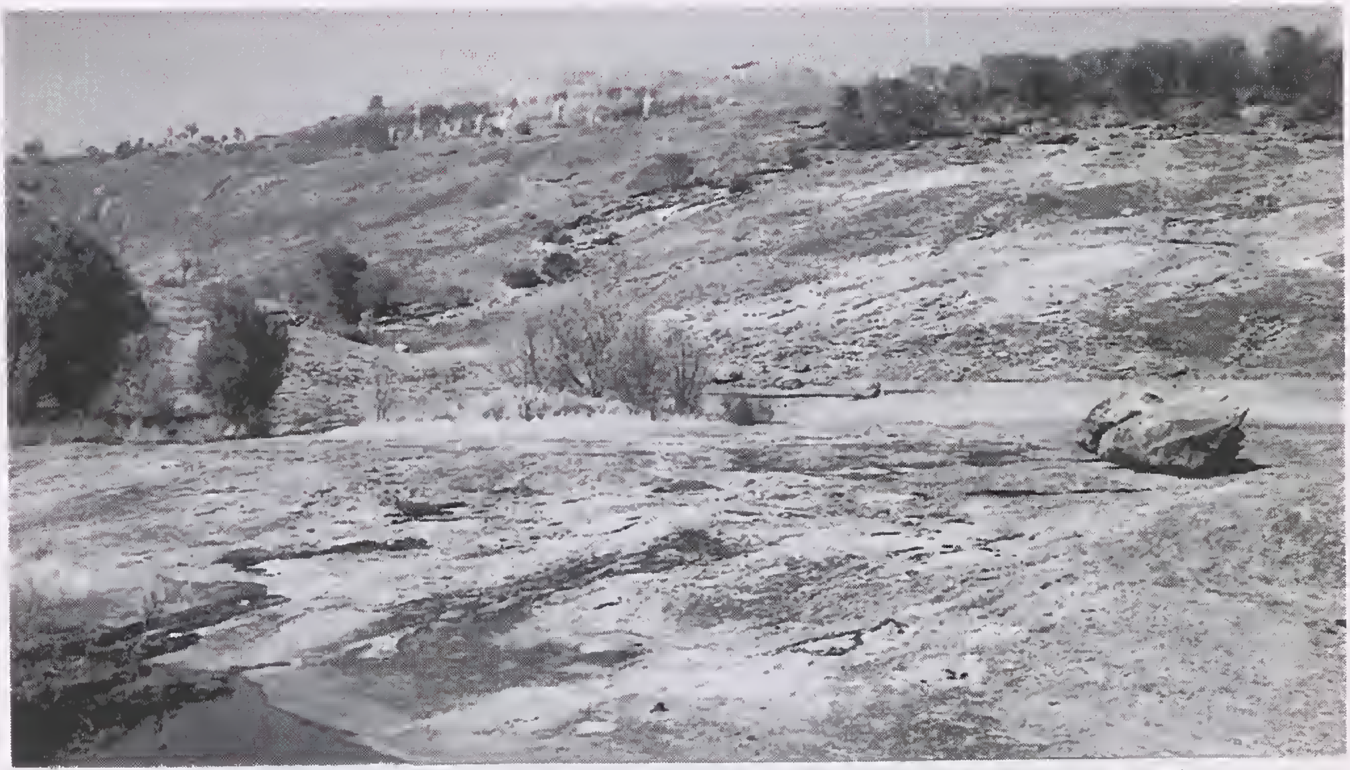


Figure 2. Southwesterly view of The Humps showing the 'entrance' valley which drains the northern sector of the hill, and its stepped morphology. The prominent flared slope high on the hill is developed below Level I, a stand of trees, on the right skyline, amidst the weathered and fractured sheet structure marks Level II. Level III is not preserved in this sector of the hill so that a gentle incline leads down from Level II to Level IV, the dry grassed areas and rock platforms of the present plain level.

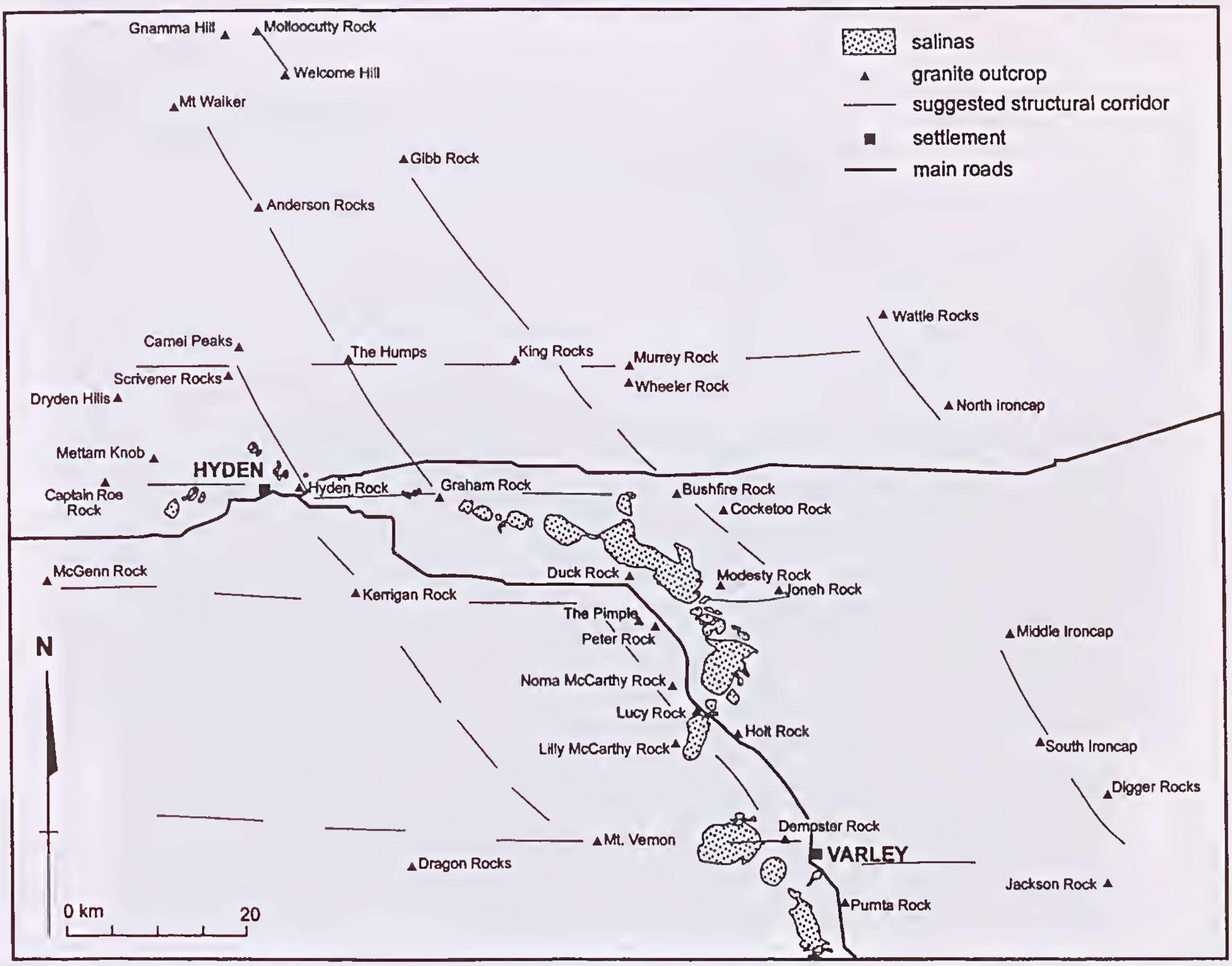


Figure 3. Structural grain in the Hyden-Varley region, part of the eastern marginal lands of the Wheatbelt, southwest Western Australia.

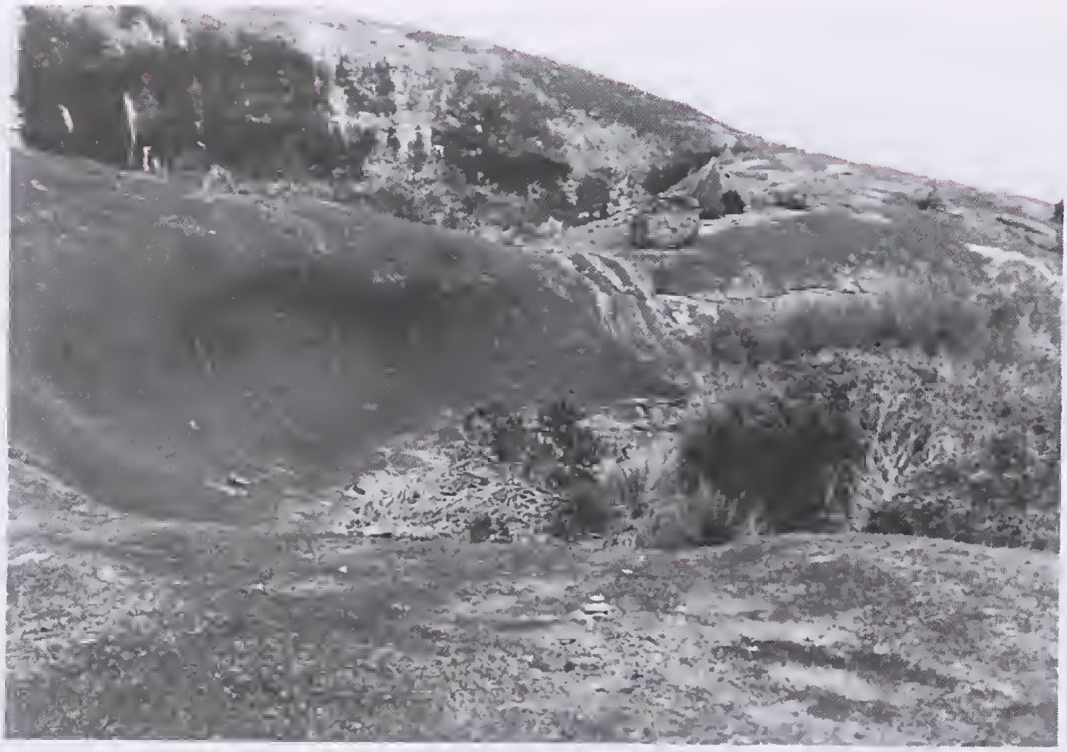


Figure 4. The northern end of the multiple flared slope is developed along a fracture zone, seen at right base of flare. Note the gently inclined fracture exposed in the slope in the middle distance, and in the foreground the flared back- and sidewalls of an armchair-shaped hollow floored with soil and vegetation.

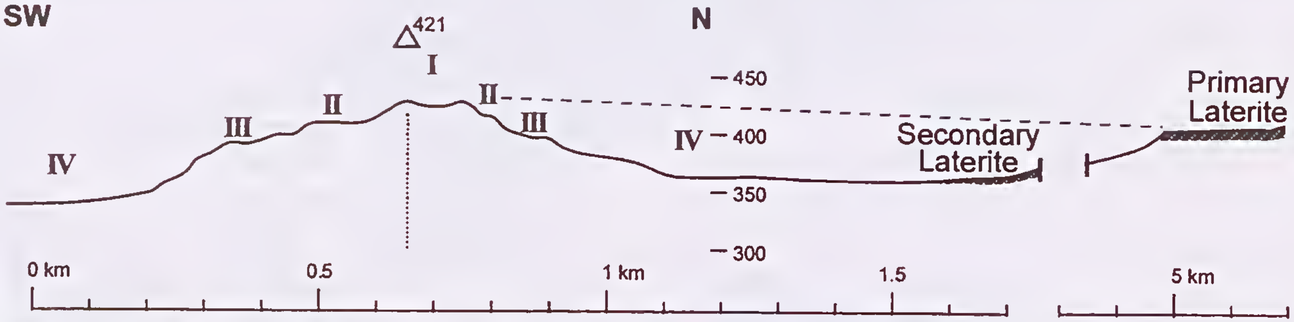


Figure 5. Diagrammatic section through The Humps showing relationship with primary laterite and secondary or derived laterite or ferricrete.

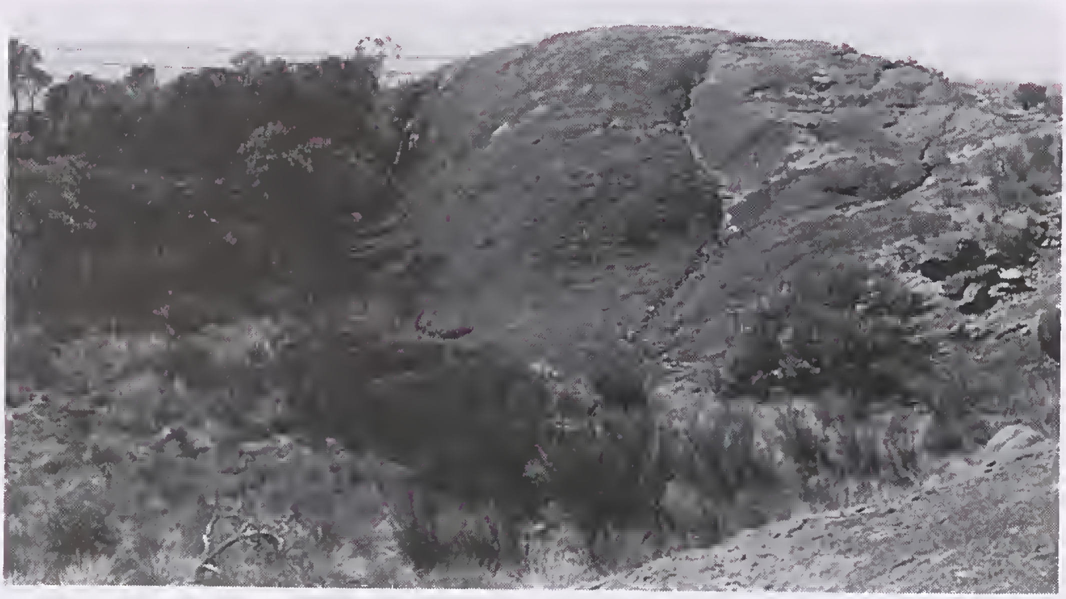
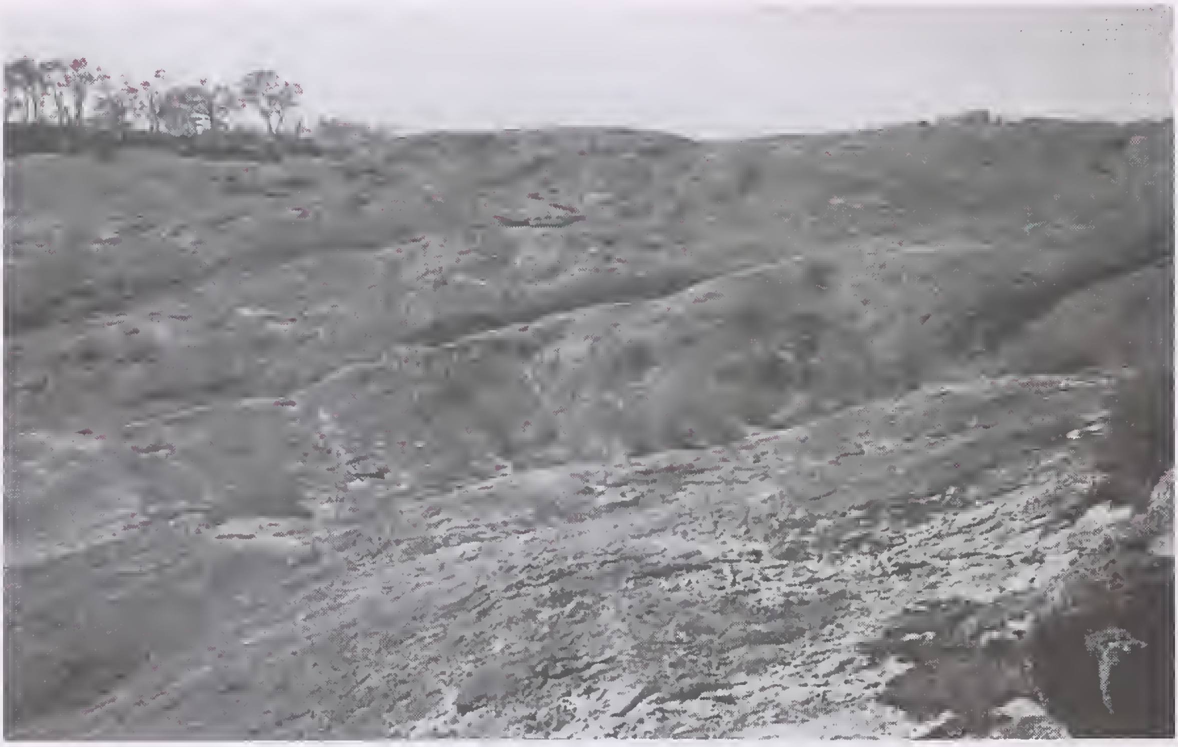


Figure 6. View southeast along the flared slope behind the stand of *Eucalyptus caesia*. Note the fractures in parallel scoring the upper and mid slopes of the dome.



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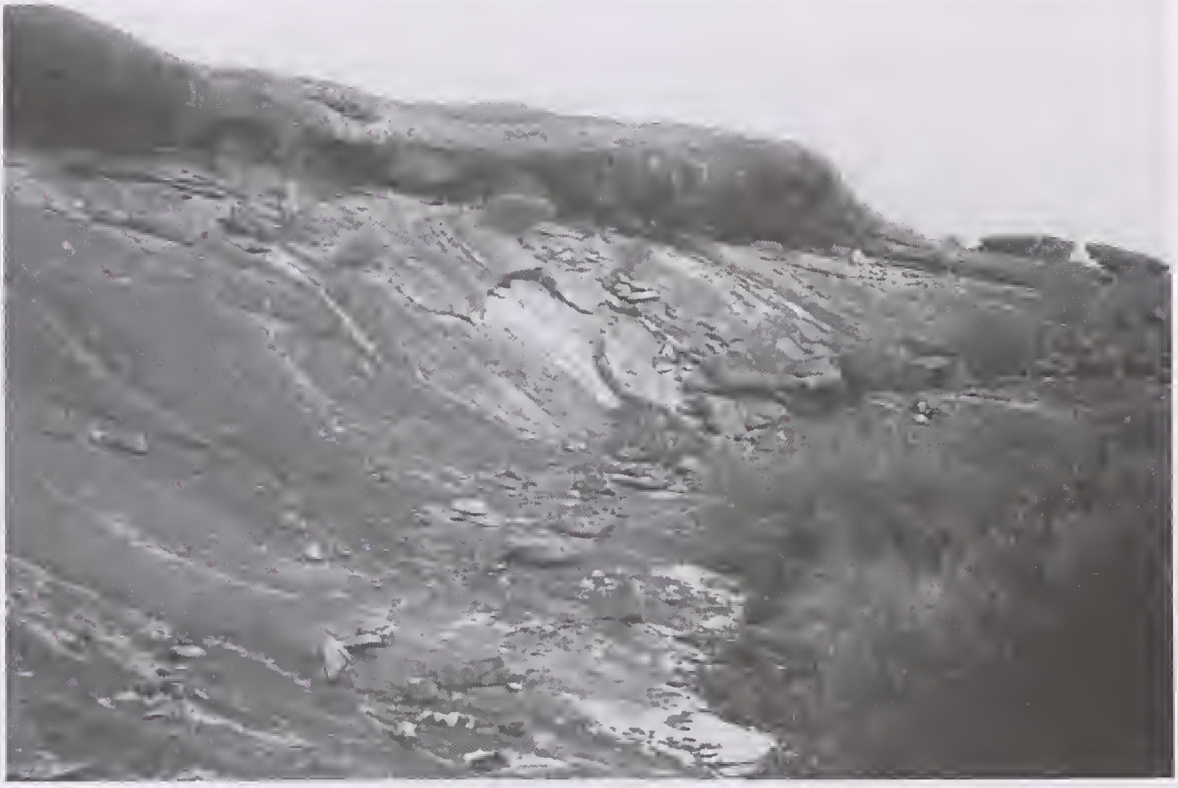


B

Figure 7. (A) View of west-facing valley-side slope where shadows emphasise major fracture lines and numerous rock basins. The wooded area of sheet remnants on the left skyline and boulders to the right mark Level II. The roughness of the granitic surface in the foreground is typical of The Humps. (B) Sheet structure exposed in a large alcove or armchair-shaped hollow on the northwestern basal slope of The Humps. Tafoni and triangular wedges occur at the base of the leading edge of the sheet structure. Note sheet remnants on right skyline, and slipped slabs near the figure. The black coating in left foreground is due to blue-green algae which favour the shallow channels carrying runoff from the slopes above. The vegetation to right has colonised the sand and clay accumulated in the floor of the alcove.

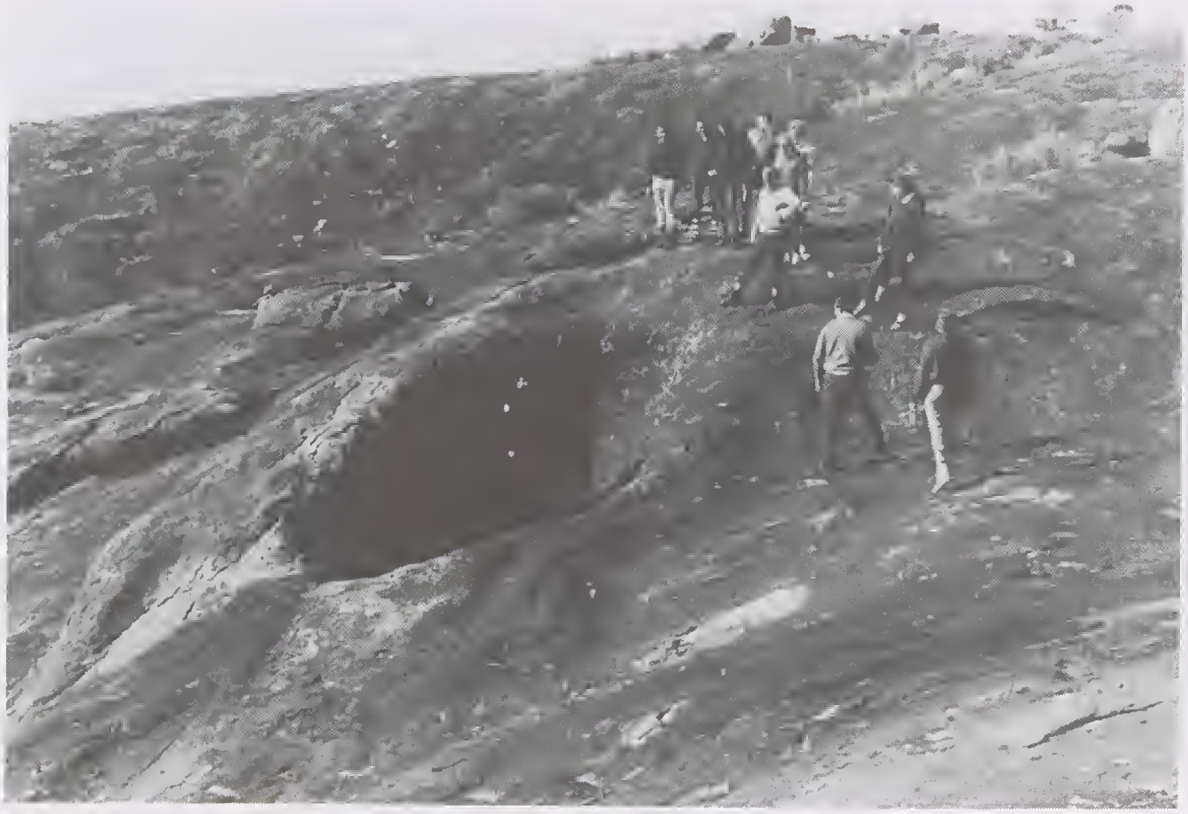


Figure 8. An unusually deep armchair-shaped hollow developed high on the midslope near the head of the entrance valley.

1960; Mabbutt 1967; Bocquier *et al.* 1977; also Ruxton 1958).

If this interpretation is correct, the dome surmounting Level II was in existence during the later Cretaceous 70–100 m.y. ago. Level I is even older, though there is no suggestion that it predates the Late Palaeozoic glaciation which affected all of what is now southern Australia (B M R Palaeogeographic Group 1992). The antiquity of levels I and II finds support in the survival in a broad joint cleft high on the eastern slope of the bornhardt (Fig 6; 4 *in* Fig 1) of *Granitites intangendus*, a monotypic genus which is at least of Middle–Late Tertiary age (Fay *et al.* 2001). Also in this cleft is a geographically isolated and genetically divergent population of *Eucalyptus caesia* (Hopper & Burgman 1983).

Structural effects and multistage development

The granitic rocks of The Humps are commonly porphyritic, and large feldspar crystals project a few millimetres, providing a pitted or rough surface (Twidale & Bourne 1976; 7 *in* Fig 1). The rocks have been sheared and fractured, resulting in prominent partings aligned roughly 130°, 140° and 160° (Fig 7A). The rock has also been intruded by veins and pods of aplite, quartz and pegmatite. Many of the veins of which the pegmatite is the youngest are aligned along fractures but there are many cross-cutting veins and numerous complex intersections are exposed, especially on the southern slopes of the residual. These fractures and intrusions have had a profound effect on the morphology of the inselberg both in gross and in detail.

Fractures strongly influence the detailed morphology of the residual, being responsible for several prominent clefts and for the deep valley on the northern flank of the residual (Fig 7A; 2 *in* Fig 1), but such features are widely spaced. Many have flared sidewalls. Sheet fractures and structures (Figs 4 & 7B) are exposed on the slopes of the residual and notably in a large alcove or armchair-shaped hollow (*q.v.*) near the western base of the hill (Fig 7B).

Linear shallow depressions are associated with steeply-dipping pegmatite sills and some locally steep slopes can be explained in terms of the preferential weathering and erosion of such gently inclined bodies (*cf* Bourne & Twidale 2002). Aplite sills have given rise to eye-catching 'boxwork patterns' (Fig 9A) as well as 'tramlines' or parallel projecting veins and irregular or wavy miniature ridges (Fig 9B; 7 *in* Fig 1). Preferential weathering and erosion of country rock infested by sills of relatively weak rock has caused them to the eroded, leaving rounded linear or gently sinuous ramparts or low ridges in relief. Zones buttressed by massive pods and veins of quartz (9 *in* Fig 1), combined with preferential weathering and erosion of pegmatitic areas have produced a cascade of basins and linking channels on the western midslope of The Humps (Fig 10).

Clearly, though The Humps and associated minor forms are two-stage developments, the origin of numerous minor features can be traced to the Archaean and to several magmatic episodes during which intrusion of various composition and textures were introduced. Considered both in gross and in detail the residual is a multistage feature (Twidale & Vidal Romani 1994).

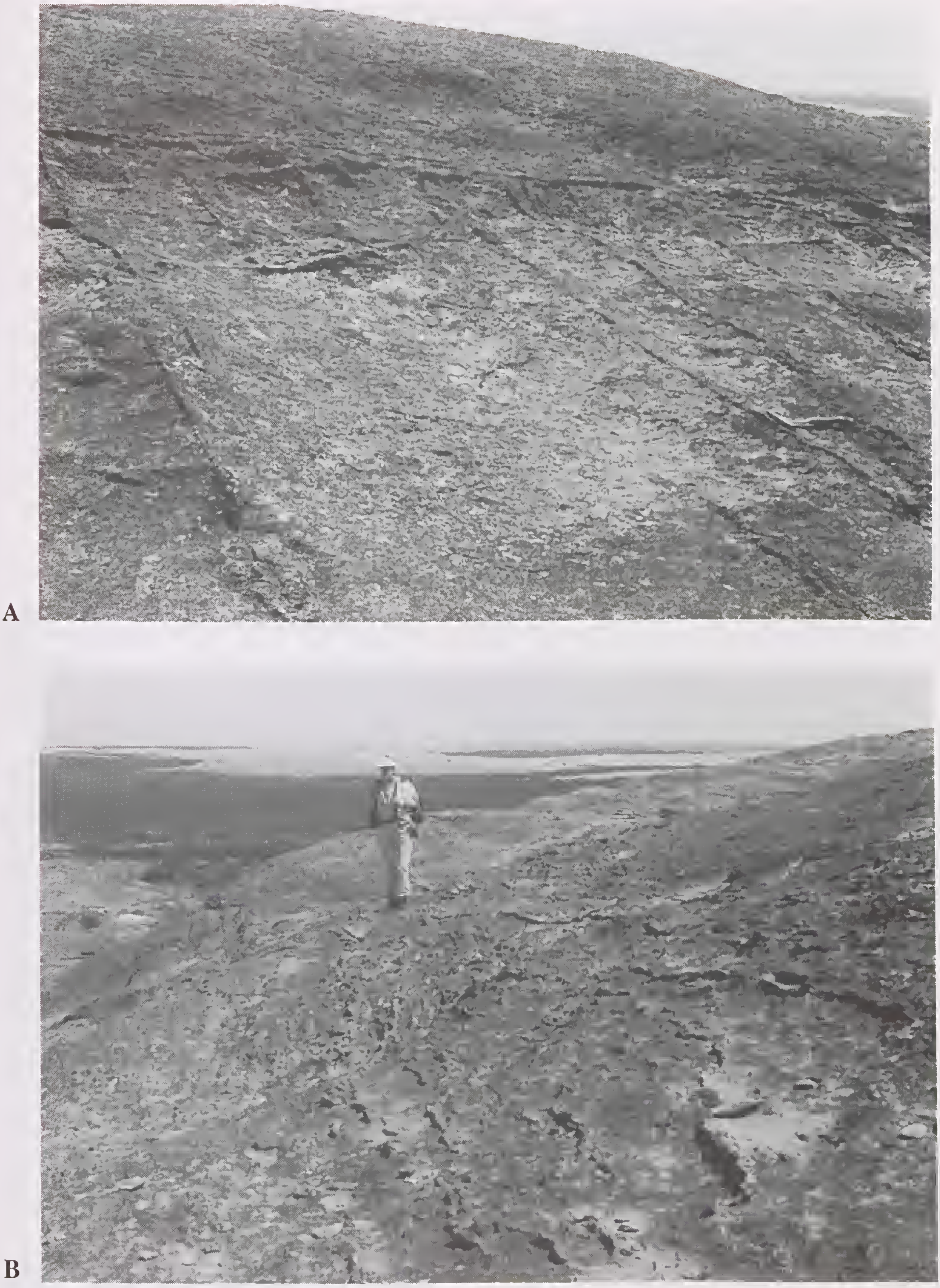


Figure 9. (A) Boxwork pattern due to greater resistance to weathering and erosion of intrusive veins, south of crestal area. Note rough surface of slope above, and porphyritic texture of rock seen in foreground. Hammer gives scale. (B) Wavy 'tramlines' to south of crestal area.

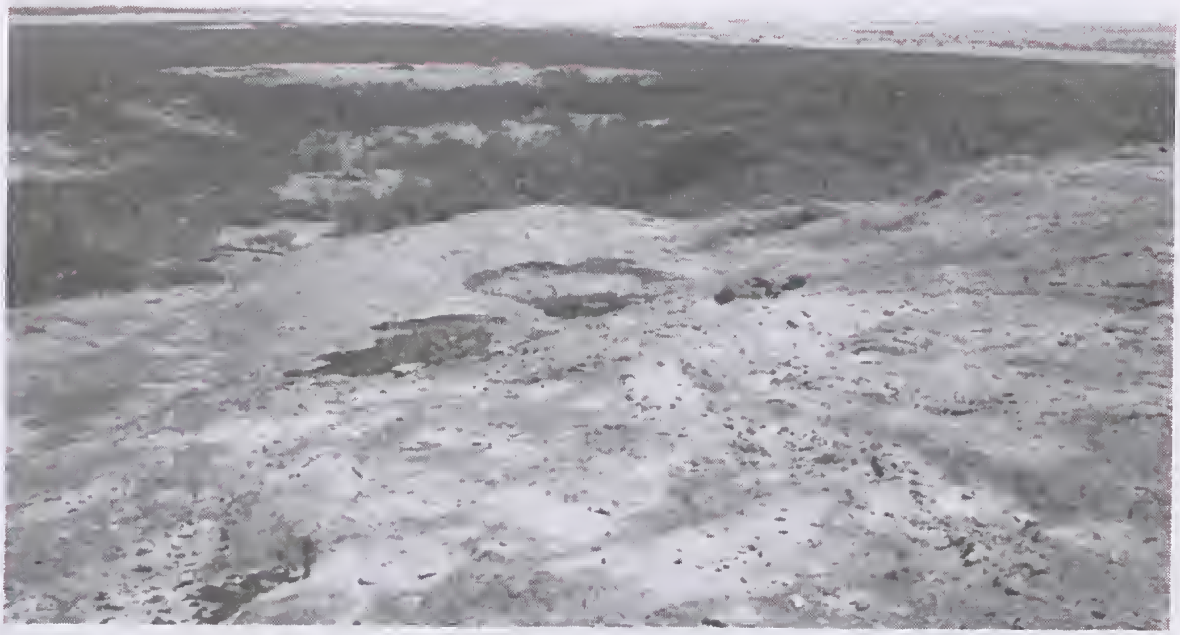


Figure 10. Cascade of rock basins draining north (away from the camera) and located between a rampart buttressed by quartz (left) and slope of the hill (right). Low rise or platform, devoid of trees, in middle distance (see separate outcrop NW of hill on Fig 1).

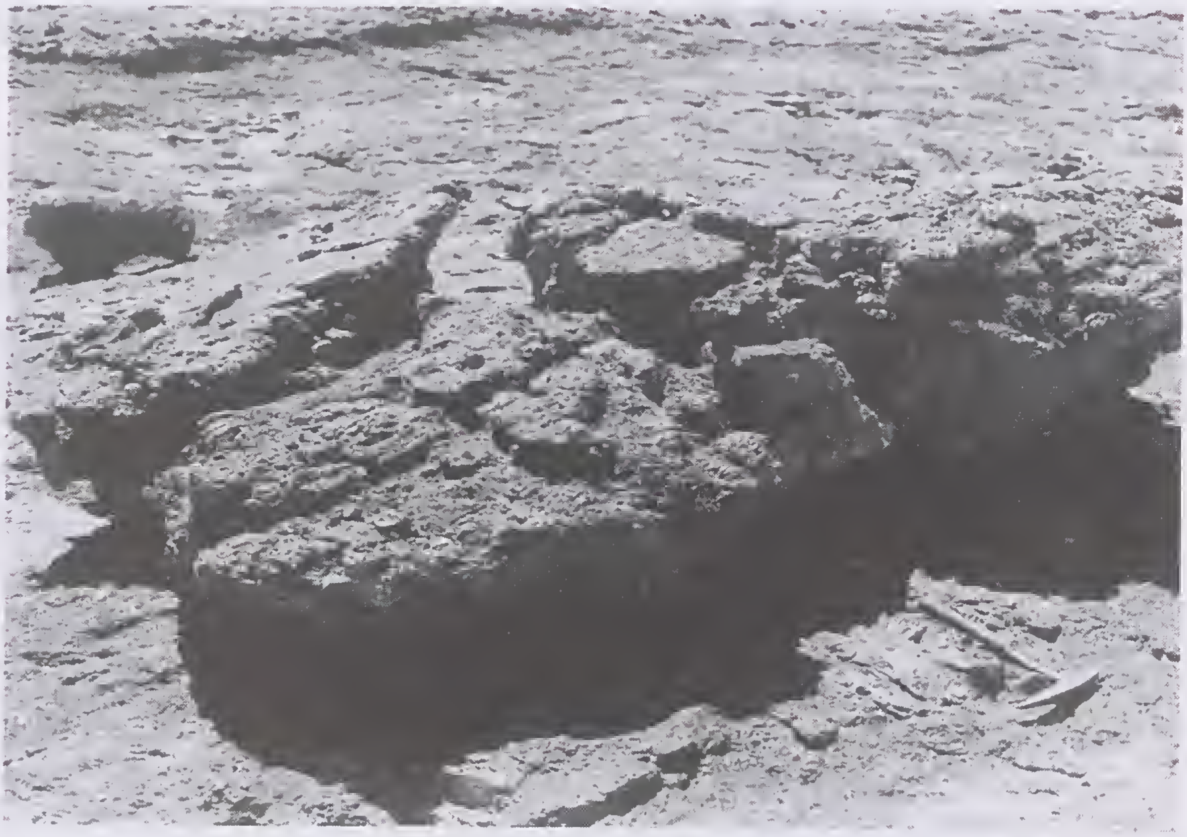
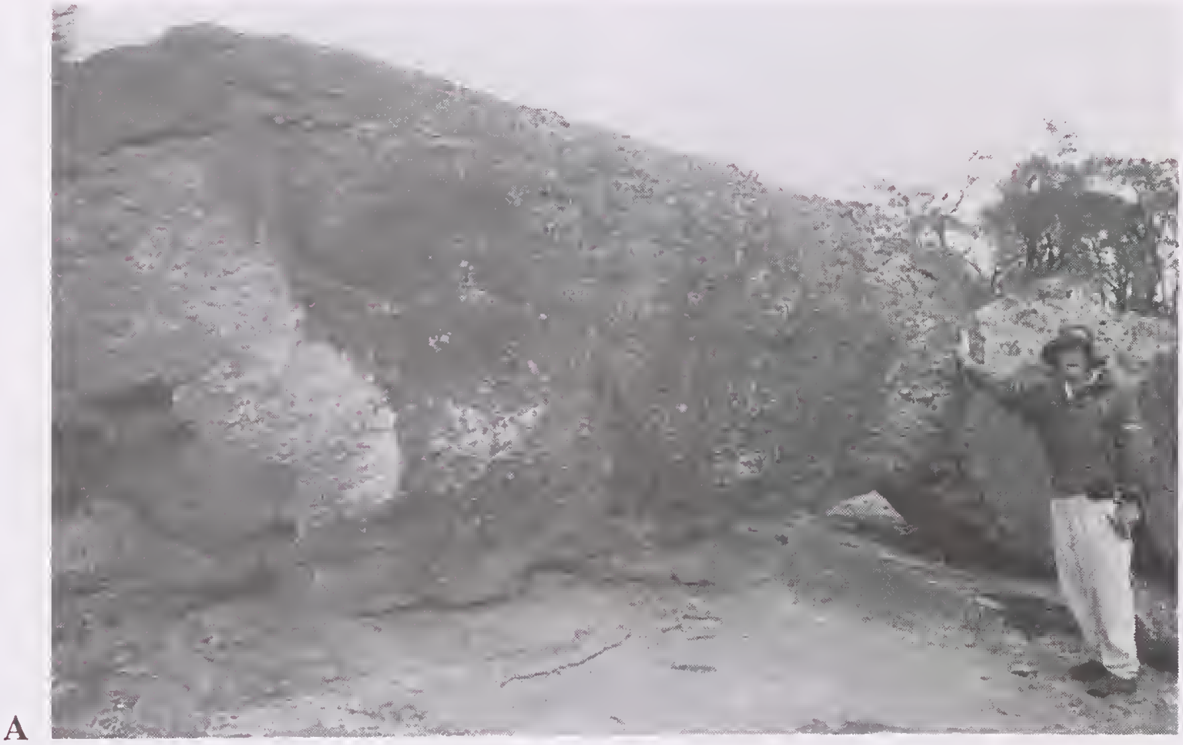


Figure 11. Weathered sheet remnant on Level II in the southwestern sector of The Humps. Polygonal cracking has been exploited and plates weathered away, leaving some polygonal remnants upstanding as 'mogotes'.

Impacts of seismic events

Though seismically stable by comparison with some parts of the world, the southwest of Western Australia is one of three relatively active sectors within the continent (*e.g.* Gordon & Lewis 1980, pp. 209–214). The formation of new fault scarps is reported from several sites from Mt Narryer in the northwest to Lort River in the southeast. The impacts of the Meckering earthquake of October 1968 are well known, evidence of active warping (as opposed to faulting has been detected in the Northam area and two periods of activity on the Hyden Fault have been identified (Thom 1972; Williams 1979; Gordon & Lewis 1980; Wellman & Tracy 1987; Twidale & Bourne 2003; Crone *et al.* 2003). Thus, it is not surprising that, like



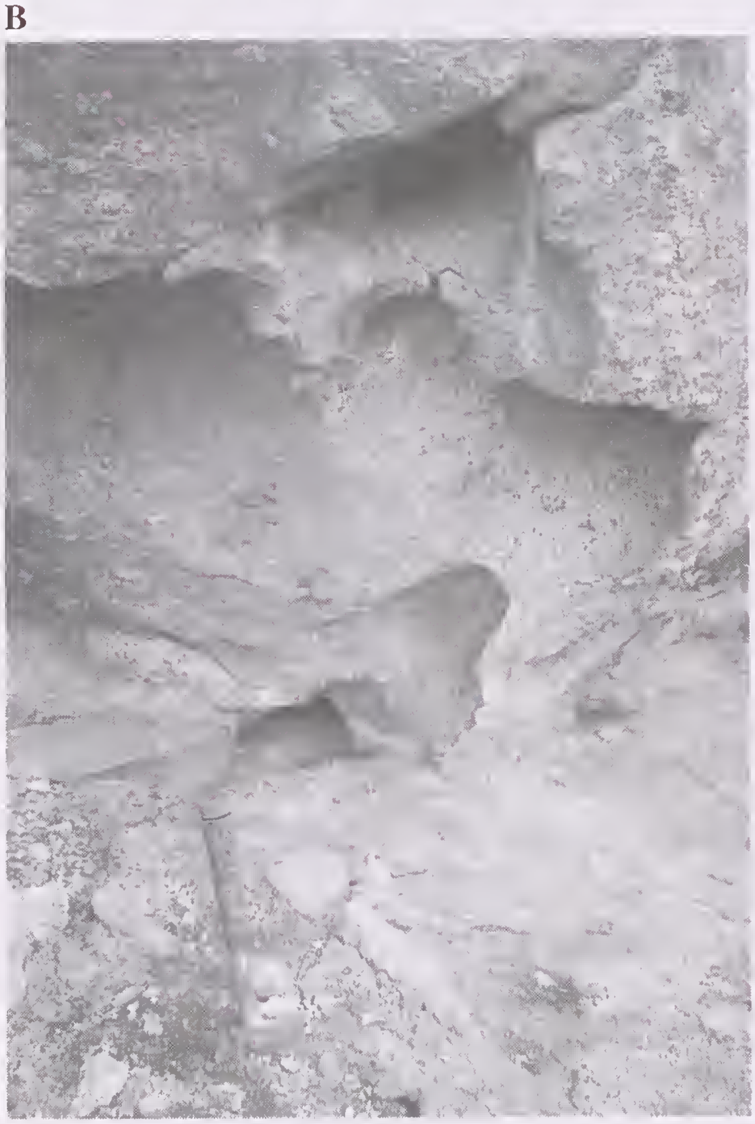


Figure 12. (A) Elongate boulder with tafone at left end, and undercut lower margins. (B) Detail of tafone with markedly mamillated surface, shown in Fig 12A. The granite is weathered and crumbles to the touch. The feldspars are altered to kaolin. Hammer provides scale.

many other massive outcrops in the vicinity, The Humps has been affected by earth movements. Evidence takes the form of an A-tent (have others been disturbed and used as small animal traps?), blisters or arches not yet with cracked crests, and several groups of slipped slabs and low angle fractures slicing though the crests of domical rises (*cf* Twidale & Sved 1978; Twidale & Bourne 2000). The formation of split rocks may have been hastened by seismic shaking.

Other specific features

Polygonal cracking and mogotes

Spectacular groups of miniature mesas, or *mogotes*, capped by iron oxide indurations occur low on the western slope of King Rocks, some 20 km east of The Humps (Twidale *et al.* 1999). It has been suggested that they are remnants of indurated polygonally-cracked surfaces which originated at the weathering front, where a concentration of iron and other oxides created a space problem, which in turn produced cracking and arching of some of the plates (Twidale 1982a, pp 315–317).

Evidence from the southern slopes of The Humps sustains this interpretation for some components of the polygonally-cracked heavily indurated surface of some residual blocks have been eroded. This can be construed as an early stage in the development of mogotes from a cracked surface (Fig 11; 8 *in* Fig 1). The encrustation is, however, not iron-rich but mainly organic. Lichens, for instance, protect the surface but also they introduce the possibility that they may have caused expansion, for instance, sufficient to buckle pre-existing thin plates as their hyphae (or rootlets) penetrated between crystals exposed in the surface layer of rock.

Subsurface initiation of tafoni and alveoles

Though many familiar major and minor granite landforms are demonstrably of two-stage or etch type and are of subsurface origin (see e.g. Twidale 1962; Twidale & Bourne 1975b, 1976) the provenance of alveoles and tafoni (Fig 12A) has remained enigmatic. On the one hand, the enlargement of the hollows is clearly due to salt crystallisation or haloclasty (Evans 1969; Winkler 1975; Bradley *et al.* 1978). Growth takes place from the base upwards in exposed blocks, boulders and sheet structures. Evidence of subsurface initiation is lacking, though the lateral merging of tafoni with flared slopes, as for example at Ayers Rock (Uluru) and at Kokerbin Hill (Twidale 1978; 1982a, p 257), suggests that some have been initiated within the regolith.

This conclusion finds support on the northwestern spur of The Humps just below but associated with Level II. There, several large residual boulders display tafoni developed in rock that is rotten due to chemical weathering of the basal zones (Fig 12B). It is suggested that the bases of the boulders, resting on an impermeable rock-base – an intact sheet of rock – were altered as a result of contact with water. The feldspars have been altered to kaolin. Limonite is concentrated in the marginal zones or visors. This chemical alteration contrasts with the haloclasty which is a physical or mechanical process and which, exploiting the already weakened host rock, is, with gravity, responsible for the formation and enlargement of the hollows.

Preservation of sheet structure and boulders on crests

The smooth outlines of the bornhardt are at several sites interrupted by isolated blocks or boulders, or by groups of such residuals preserved on crests or upper slopes (Figs 2 & 7A). The reasons for the survival of these remnants of sheet structures (10 *in* Fig 1) are twofold. First, that the volume of runoff increases downslope, so that crestal zones are less weathered and eroded than downslope areas. Downslope wash removes the *grus* which otherwise would retain moisture and thus ensure the continuation of weathering and the eventual disintegration of the blocks and boulders. Second, the lower zones have been subjected to successive phases of subsurface scarp-foot weathering. Any remnant blocks and boulders on lower slopes either have survived because they are especially large and therefore persistent, or they have fallen to their present position.

Large gnammas on crests

In the sense of areal extent, and as on many other granite hills in the district, most of the largest gnammas, in the form of shallow, flat-floored pans (Twidale & Corbin 1963), are found on the crests of hills. Some on the crest of King Rocks, for instance, are more than 15 m diameter. As runoff increases downslope (see above), it might be thought that the largest gnammas ought to be developed on lower slopes. But there, heavy runoff ensures that the basins are filled to overflowing. Egress channels are eroded, so that lateral extension by solution, hydration and hydrolysis of the rock-forming minerals by standing water is limited. On hill crests, however, only direct rainfall which stands in basins is received. Moreover, the crests are the oldest, and longest exposed, parts of the outcrops; there has been time for pans to extend laterally by moisture-related weathering.

Alcoves: armchair-shaped hollows and embayments

Several armchair-shaped hollows are developed high on the midslope of the valley which drains the northern sector of The Humps (Figs 4, 7A & 8). One is as deep as it is long and wide (Fig 8; 3 *in* Fig 1), but they are typically much wider than they are in plan dimensions.

How have they formed? Grus is washed into the floors of clefts (or slots) and valleys. There, the patches of detritus become vegetated and a soil develops. Thus a depression – an incipient alcove? – filled with enough soil to nurture small trees has formed in the floor of the cleft with *Eucalyptus caesia*. Vegetated soil patches retain moisture which aggressively react with the granite with which it is in contact by virtue of chemicals released by weathering and organic acids derived from rotting organisms. In addition, lichens favour wetter surfaces such as are found in valleys and even otherwise bare rock surfaces are attacked by the hyphae of lichens and by the roots of trees and shrubs. In these ways weathering causes vertical rotting and thickening of soil patches. They also effect lateral extension. Headward extension takes place causing steepening of the valley headwalls but lateral growth – what Mabbutt (1966) called mantle-controlled planation – takes place at both margins so that the depression widens twice as rapidly as it extends headwards. This produces alcoves or armchair-shaped hollows, some of them many tens of metres across. The side- and head-walls are commonly flared (as on Hyden Rock: Twidale & Bourne 2001) though the largest such alcove located on the western side of The Humps is bounded by slightly overhanging bluffs in which sheet fractures and structures are exposed (10 *in* Fig 1). These fractures attract weathering, so preventing any tendency for the development of a smooth convexity.

Conclusion

The Humps displays many morphological features in common with other Wheatbelt inselbergs: it is of etch origin and has survived by virtue of its massive structure, its crestal area is of great antiquity, it has been exposed in stages, and it displays many familiar minor forms including some due to contemporary seismicity. Yet it offers enough different forms and lines of evidence to make it interesting. A subsurface initiation for tafoni is suggested, the survival of the inselberg can be construed as tectonic, and the origin of several minor structural features can be traced back more than 2.5 billion years to the origin of the rock of which the inselberg is composed.

Acknowledgements: The authors thank the Hyden-Karlgarin and District Landcare group for facilitating their most recent work on The Humps and environs, and those several local enthusiasts, and notably Russel and Val Mouritz, who have actively promoted the natural features of the Hyden district for tourist and educational purposes.

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Fruit and seed development in two *Hakea* species (Proteaceae)

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Abstract

Hakea erinacea and *H. trifurcata* are related taxa that release their annual seed crop within a year of fruit maturity (weak serotiny). Both species produce similar-sized woody fruits (follicles) that protect two winged seeds. Fruit and seed development was completed 180 days (*H. erinacea*) and 215 days (*H. trifurcata*) after anthesis, with the fruits of both species reaching their maximum fresh mass during their 'green', non-woody state. This was associated with the commencement of wood formation in their fruit walls and the redistribution of certain nutrients (particularly phosphorus) from the fruit to developing seeds. Both *H. erinacea* and *H. trifurcata* retain chlorophyll in the walls of developing fruit, with *H. trifurcata* retaining chlorophyll in the mature fruit. This may have anti-herbivore properties whereby the developing green fruits are cryptically disguised within a background of similarly green leaves.

Keywords: fruit chlorophyll, seed nutrients, seed protection, woody follicles

Introduction

Hakea erinacea Meissn. and *H. trifurcata* (Smith) R.Br. are related taxa (Barker *et al.* 1999) producing relatively small fruits (130–180 mg dry mass) compared with other species in the genus (Groom & Lamont 1996, 1997). Both species are weakly serotinous (minimal canopy seed storage) (Midgley *et al.* 1991), releasing most of their seeds annually from woody fruit (follicles) that open within a year of fruit maturing (Lamont *et al.* 1998, Groom *et al.* 2001). Each follicle possesses a longitudinal adaxial suture, which when ruptured exposes two valves each containing one compressed winged seed.

Hakea fruits remain green from anthesis to near maturity, except for those species that develop very large woody follicles (e.g. *H. platysperma*). Previous work on the seed and fruit development of the closely related genus *Grevillea* suggests that translocation of mineral nutrients from the fruit to seeds occurs as the fruit matures (Hocking 1981, 1982). Proteaceous seeds are packed with nutrients (Pate *et al.* 1986) and parent plants are efficient in redistributing essential nutrients from their fruits to their seeds and hence to their seedlings (Kuo *et al.* 1982, Lamont and Groom 2002).

An understanding of fruit and seed development will provide an insight into changes in nutrient content and biomass that occur as *Hakea* fruit develop woody walls. This paper records the development of fruits and seeds from anthesis to fruit maturity within two ecologically similar *Hakea* species (*H. erinacea* and *H. trifurcata*). The onset of wood formation (i.e. transition from the non-woody 'green' state) will be assessed in terms of changes in fresh and dry mass, partitioning of selected nutrients (N, P, K, Ca, Mg) between fruit and seeds, and chlorophyll content of the fruit wall.

Materials and Methods

Fruits were collected from a population (approximately 150 plants) of *H. erinacea* shrubs in the *Corymbia calophylla-Eucalyptus wandoo* woodlands of John Forrest National Park (31°37' S, 115°51' E) between August 1992 and February 1993. *H. trifurcata* fruits were collected from a stand (approximately 80 plants) in similar woodlands at Crystal Brook Reserve (31°59' S, 116°04' E), Kalamunda, between October 1992 and March 1993. By counting annual stem increments, plants in each population were estimated to be 15–20 years old. Fifty fruits per species were collected fortnightly beginning at the end of flowering (anthesis), with each collection representing a progressive stage of fruit development. Fruits were considered to be mature when there was no change in their dry mass and they contained fully developed seeds. For each collection, fruits (with seeds) had their fresh mass and dry mass (dried for 48 h at 60°C) recorded. After 90–100 days of development seeds were easily extracted from the developing fruit and weighed separately.

For each collection, dried fruit and seed samples (including the wing) were ground and analysed for selected nutrients (N, P, K, Ca, Mg) by CSBP and Farmers Co., Perth based on 0.8 – 2 mg samples. N was determined by standard Kjeldahl digestion on bulked samples, whereas the remaining nutrients were determined from digestion in 9:1 nitric/perchloric acid. P was determined colorimetrically and cations (K, Ca, Mg) by atomic absorption spectrophotometry. Chlorophyll was extracted from five weighed samples per collection (5–10% w/v) of fruit material in *N,N*-dimethyl formamide and analysed spectrophotometrically using the extinction coefficients of Moran (1982).

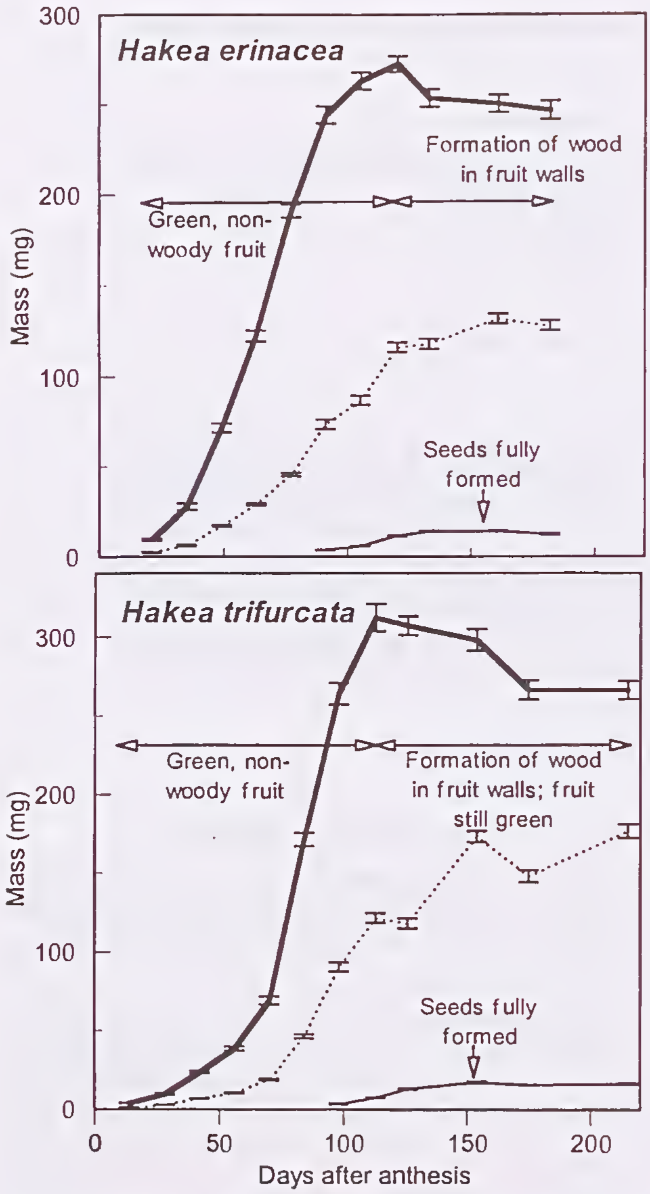

Figure 1. Fresh (thick solid line) and dry (dashed line) weight of fruit, and dry weight of seeds (thin solid line) during annual fruit development of *H. erinacea* and *H. trifurcata*. Data represent mean (± SE) from 50 fruits per species.

Results

Hakea erinacea fruits took 180 days to reach maturity, with wood formation in the fruit walls commencing 120 days after anthesis (Fig. 1). The similar sized *H. trifurcata* fruits took 215 days to reach maturity, with wood formation initiated after 110 days (Fig. 1). *H. trifurcata* seeds were slightly larger (16.4 ± 2.4 mg dry weight) than those of *H. erinacea* (12.5 ± 2.8 mg), although both species had similar final seed-to-fruit weight ratios (0.19; based on two seeds per fruit). Seeds were fully formed after 154 (*H. trifurcata*) and 161 (*H. erinacea*) days of development, 40 days after the commencement of fruit wood formation. Both species retained chlorophyll in their fruit walls during the non-woody ('green') phase of development. For *H. erinacea*, total fruit wall chlorophyll content stabilised around 0.24 mg g^{-1} between 40 to 133 days (Fig. 2), whereas *H. trifurcata* chlorophyll content decreased with an increase in developing fruit size. Chlorophyll content of developing fruit was approximately one-third of leaves (0.6–0.9 mg g^{-1}). Chlorophyll was present in the walls of mature *H. trifurcata* fruits (0.09 mg g^{-1}), but not in the fruit walls of *H. erinacea*.

Of the five nutrients investigated, the total fruit nutrient content (in mg) for *H. erinacea* was near zero 21 days after anthesis (N: 0.039; P: 0.0004; K: 0.02; Ca: 0.032; Mg: 0.0009). These increased to a maximum 105 days (N: 1.18), 120 days (P: 0.017) and 160 days (K: 0.13, Ca: 0.06, Mg: 0.02) after anthesis (Fig. 3). For K, Ca and Mg, this was approximately 20 days before the onset of fruit wood production. Once fruit wood formation had commenced, the total nutrient content (in mg) of one *H. erinacea* seed (N: 1.18, P: 0.14, K: 0.11, Ca: 0.18, Mg: 0.05) was less than (N, P) or greater than (K, Ca, Mg) the amount present in a fully developed seed (Fig. 3). Calculating apparent translocation of each nutrient from the follicle as it

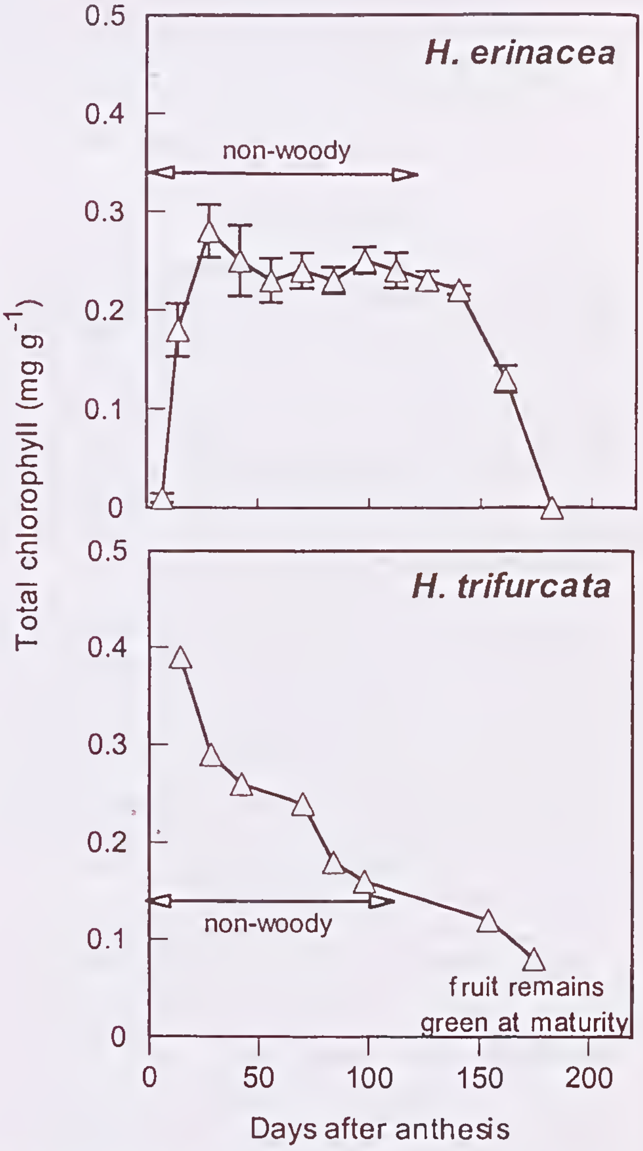

Figure 2. Total chlorophyll content of the fruit wall during annual fruit development of *H. erinacea* and *H. trifurcata*. Arrowed-line represents period during fruit development when fruit were fleshy and non-woody. Data represent mean (± SE) from 5 fruits per species.

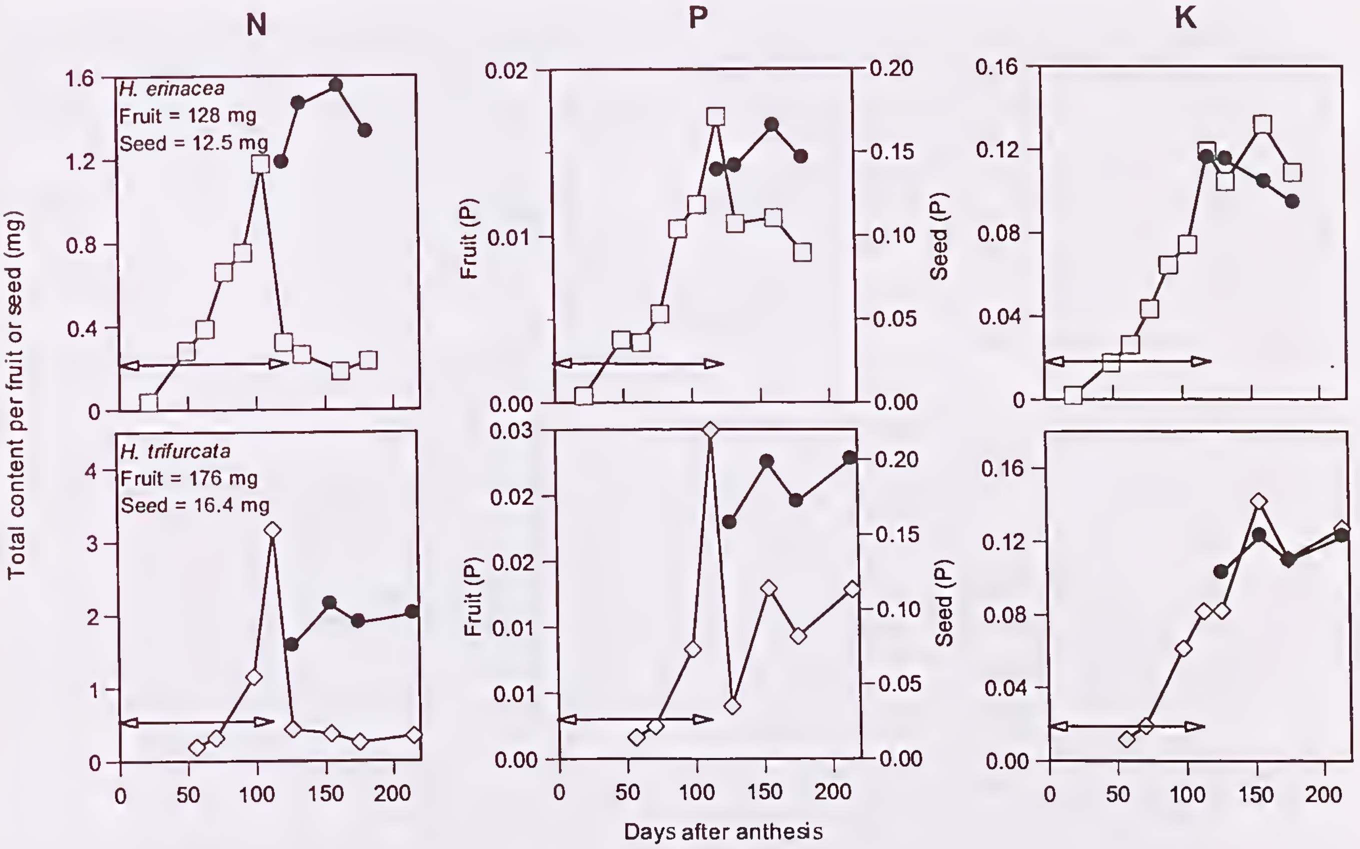

Figure 3. Total nutrient content of N, P and K in the fruit (open symbol) and seed (filled symbol) of *H. erinacea* (top row) and *H. trifurcata* (bottom row). Ca and Mg show similar trends as K. For P, fruit and seed data are on separate axes. Arrowed-line represents period during fruit development when fruit were fleshy and non-woody. Data calculated from the average fruit dry mass and the dry mass of one seed.

matured (after Hocking 1982) showed that N and P were redistributed with the greatest efficiency (80% and 48% respectively) and K, Ca and Mg with much less efficiency (0.5–19%). A decrease in total fruit nutrient content was associated with the onset of wood formation in the fruit walls of *H. erinacea* (Fig. 3).

The total nutrient content (in mg) in the fruit of *H. trifurcata* reached a maximum 110 days after anthesis (Fig. 3) and was synchronised with the beginning of fruit wood formation. The total fruit nutrient content (in mg) for *H. trifurcata* reached its maximum (N: 3.17; P: 0.025; Ca: 0.56; Mg: 0.24) 115 days after anthesis (Fig. 3). Potassium peaked at 0.14 mg 150 days after anthesis. At the commencement of fruit wood formation the total nutrient content of one *H. trifurcata* seed was less than (N, P, Mg) or greater than (K, Ca) the amount present in a fully developed seed (Fig. 3). Redistribution efficiency of nutrients translocated from maturing follicles to seeds in *H. trifurcata* was low for K and Ca (10–15%), moderate for N and Mg (24–32%) and high for P (63%).

Discussion

Hakea erinacea and *H. trifurcata* have similar fruit and seed size, and produce mature fruits and seeds within similar developmental time-frames. The fruits of both species reached their maximum fresh mass during their 'green', non-woody state, occurring with the commencement of wood formation in their fruit walls. Developing fruits are an important store of essential nutrients (*e.g.*, N, P) (*cf* Hocking 1981, 1982) that were translocated to the two winged seeds at the onset of fruit wood formation. Within the Proteaceae, woody fruit protect the seeds from external damage by heat, desiccation and granivores, as well as providing an economical method of redistributing certain nutrients to the developing seeds (Stock *et al.* 1991, Lamont & Groom 1998).

The timing of fruit wood formation in *Hakea* follicles may be related to fruit size, which in turn is a function of the ability of the species to store seeds within their canopy (serotiny). Weakly serotinous *Hakea* species typically possess smaller, thinner walled follicles with less dense wood than more serotinous species (Groom & Lamont 1997). By allocating a relatively small amount of carbon (130–180 mg dry weight) into their thin woody fruit walls, the weakly serotinous *H. erinacea* and *H. trifurcata* provide limited seed protection over a relatively short period of time, without affecting the efficiency with which certain nutrients are redistributed to the developing seeds. For fire-prone plant species, weak serotiny has evolved because costs (carbon invested in protection) outweigh the benefits (maximising recruitment) (Midgley 2000). Differences between maturation time and degree of serotiny is supported by Hocking (1982) who showed that the non-serotinous, leathery follicles of *Grevillea wilsonii* matured within 9 weeks of anthesis, compared with the 25 weeks of the serotinous, woody fruit of the co-occurring *Hakea undulata*.

Both *H. erinacea* and *H. trifurcata* retain chlorophyll in the walls of developing fruits, with only *H. trifurcata* retaining chlorophyll in the mature fruit. This may enable the developing fruit to provide its own supply of photosynthates, although it is more likely that leaves are a major source of carbon for fruit and seed growth. Green developing fruits may have anti-herbivore properties, akin to the cryptic mimicry experienced by the mature fruit of *Hakea trifurcata* (Groom *et al.* 1994), and other weakly serotinous species (e.g. *H. prostrata*), whereby the developing green fruit are disguised within a background of similarly green leaves.

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Sedimentary fill of basin wetlands, central Swan Coastal Plain, southwestern Australia. Part 1: sediment particles, typical sediments, and classification of depositional systems

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Abstract

The common sediments in wetland basins occurring in the Spearwood Dunes, Bassendean Dunes and Pinjarra Plain of the central Swan Coastal Plain, southwestern Australia are peat, diatomite, calcilutite (carbonate mud), their intermediates such as diatomaceous peat, organic enriched diatomite or calcilutite, and carbonate skeletal gravel and sand (all formed by biogenic processes), as well as quartz sand and kaolinite-dominated mud (as terrigenous sediments), and various types of muddy sand formed as mixtures between biogenic mud-sized sediments and quartz sand, or between kaolinitic mud and quartz sand. Synsedimentary processes and diagenesis result in local cementation, desiccation, and reworking of these deposits, particularly along the margins of wetland basins, and hence the development of carbonate intraclast gravel and sand, diatomite intraclast gravel and sand, and peat intraclast gravel and sand. A clear distinction is made between wetland sediments and wetland soils, and between primary wetland sediments and the products of diagenesis within and around wetlands. Gravel-sized particles in the wetland sediments include plant remains, invertebrate faunal skeletons, and intraclasts. Sand-sized particles include plant remains, quartz, invertebrate faunal skeletons, and intraclasts. Petrographic microscopy and scanning electron microscopy show the < 63 µm particles that comprise the sediments are plant remains, diatom frustules and fragments, sponge spicules and fragments, aggregates of calcite crystals derived from charophytes and the disintegrated clay-sized derivatives of these charophytic aggregates, comminuted invertebrate skeletons, quartz silt, and mud-sized phyllosilicate minerals.

Wetland sediments can be categorised as to origin, *i.e.*, biogenic *versus* terrigenous, as to whether they are end-member primary sediments, or derivatives, or mixtures, as to their location of formation relative to the basin, *i.e.*, intrabasinal, autochthonous *versus* extrabasinal, allochthonous, as to their infiltrational and accretionary nature in relation to the basement material, and as to their location within a basin, *viz.*, central basin *versus* marginal *versus* basal deposits.

Keywords: wetland sediments, peat, diatomite, calcilutite, Swan Coastal Plain wetlands

Introduction

Wetlands, as natural topographic depressions in the landscape, fill with sediment, and as a result, globally, they are known to be important reservoirs of information on geohistory, geochemical history, vegetational succession and palaeoclimate (Barber 1981; Druckman *et al.*, 1987, Gasse *et al.*, 1987; Talbot 1990; Baltzer 1991; Odgaard 1992; Leaney *et al.*, 1995; Wright and Platt 1995; Fritz *et al.*, 1999). The wetlands on the Swan Coastal Plain of the Perth Basin are prime examples of such archives as they contain vast and variable information in their sedimentary sequences. They have the potential to encode Holocene geologic, hydrologic, and hydrochemical history, vegetation changes, and climate changes, as preserved in their stratigraphic, diagenetic, isotopic, faunal, and floral records.

While there is mention and some description in the literature on the central Swan Coastal Plain of types of wetland sediments, their stratigraphic expression, and their local thickness (Simpson 1903; Teakle & Southern 1937; Allen 1979; Megirian 1982; Hall 1983; Muir 1983; Hall 1985; Semeniuk 1988; Newsome & Pickett 1993; Coshell & Rosen 1994; Pickett 1998), to date, these sediments have not been subject to a systematic or comprehensive description. This paper, the first in a series on wetland sediments of the Swan Coastal Plain, describes the particle types that comprise the wetland sediments in this region, describes the main sediment types, and provides an interpretation of their origin. It also provides a preliminary outline of wetland sediment diagenesis in order to clearly separate primary sediments from diagenetic products. The stratigraphy and the age structure of sedimentary fills in wetland basins will be the subject of later papers (Semeniuk & Semeniuk 2005 a). The scope of this paper is limited to those isolated wetland basins across the central Swan Coastal Plain, between Moore River and the Mandurah/Pinjarra region, mainly within the settings of the Spearwood Dunes, Bassendean Dunes and those local parts of the Pinjarra Plain that are not directly connected to fluvial systems

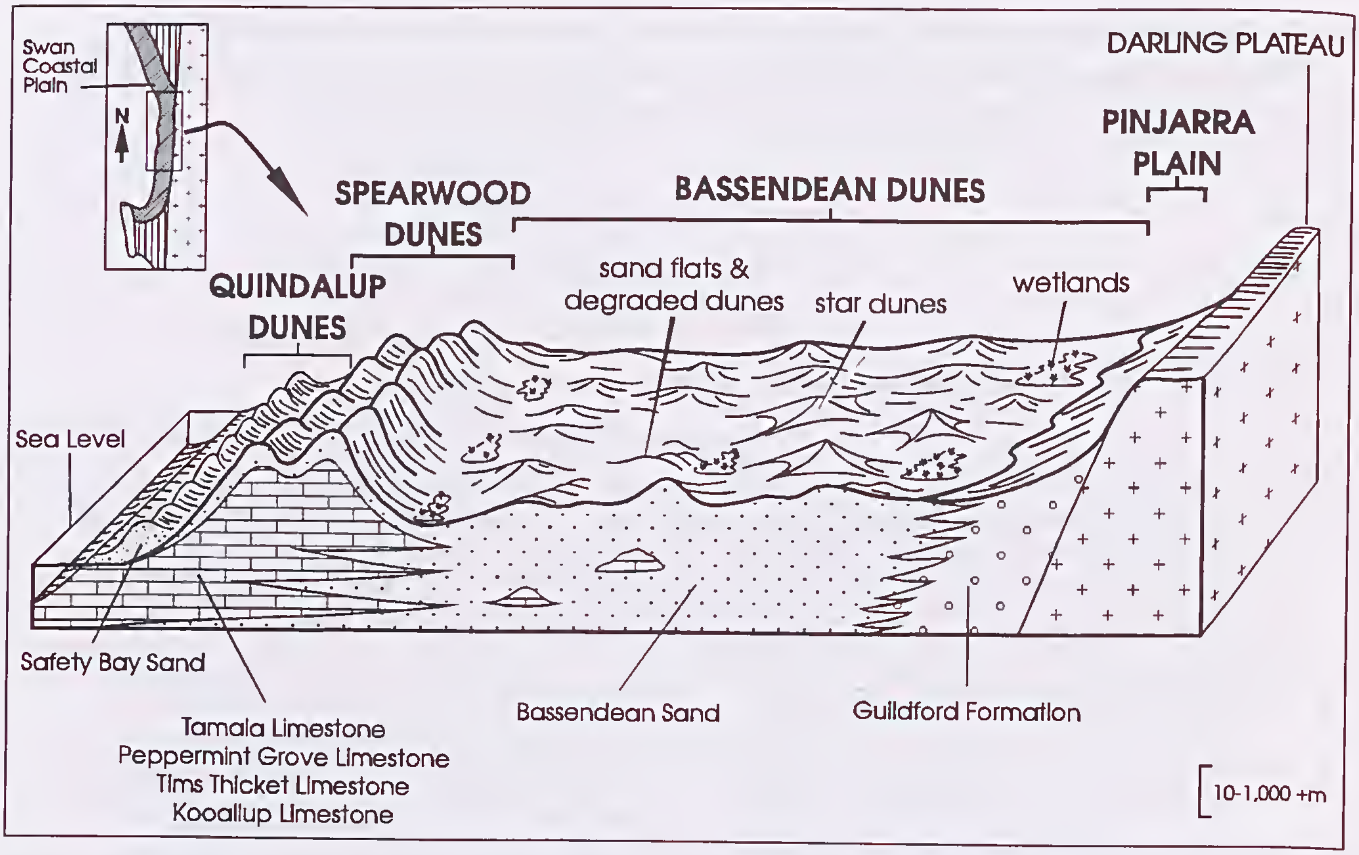


Figure 1. Idealised block diagram showing geomorphic units of the Swan Coastal Plain, their sub-parallelism to the Darling Scarp and the coast, their gross surface features, and their stratigraphy, with some details of landscape (after Semeniuk & Glassford 1989). The scope of this study involves only the Spearwood Dunes, Bassendean Dunes, and parts of the Pinjarra Plain.

(Fig. 1). The linear wetlands of the Yalgorup Plain (Semeniuk 1995) of the central to southern Swan Coastal Plain will be the subject of a separate study. Wetlands within the Becher Suite of the Quindalup Dunes of the central Swan Coastal Plain also are the subject of a separate study (Semeniuk 2005), though for completeness brief mention is made in this paper of some of their deposits in terms of the nomenclature used herein. Beachridges and lunettes that have formed along the margins of wetland basins, and that have become emergent above the high-water mark are not treated as part of the wetland fill deposits in this paper. The sediments of fluvial wetlands and related features (*i.e.*, channels and floodplains), whose landform surfaces range in age from Pleistocene to Holocene, as well as estuaries and linear lakes and lagoons formed leeward of marine-derived barriers also are not considered in this paper. Sedimentation in selected linear lagoons and estuaries marginal to the Swan Coastal Plain has already been described in Semeniuk & Semeniuk (1990), and Semeniuk (1996, 2000).

Classification and terminology

The wetland classification of Semeniuk (1987), developed for the central Swan Coastal Plain, is used in this paper. This classification uses the components of landform and hydrologic regime to develop wetland categories. As the emphasis in this paper is on basin wetlands, only the terms for these are noted here. Combining basin landform with hydrologic regime in the Swan Coastal Plain results in 3 categories of wetland: 1. permanently inundated basin = lake; 2. seasonally inundated basin = sumpland; and 3. seasonally waterlogged basin = dampland. Water and landform descriptors augment the primary categories.

In this paper, the term *intraclast* is extended from the usage of Folk (1962), who coined it for intraformational clasts in carbonate depositional regimes, to refer to any reworked clasts of cemented, indurated, or dried sedimentary materials that belong to the cycle of sedimentation in which they are embedded. Intraclasts may be gravel sized to sand sized. The term *intraformational* describes production of particles that form *within* a given sedimentary formation. For example, the cementation, reworking into clasts, and incorporation of these clasts into extant sediments are intraformational phenomena. The term *infiltrational* describes deposits that form by infiltration into another sedimentary formation. For example, the delivery by vadose processes resulting in the accumulation of fine-grained sediments interstitially *within* another sedimentary body, rather than superposed *on* that body, is an infiltrational phenomenon. The term *accretionary* describes deposits that accumulate vertically by superposition above another sedimentary formation. The term *synsedimentary* refers to processes that occur concurrently or penecontemporaneously with sedimentation. Burrowing by fauna, and root-structuring by vegetation, contemporaneous or penecontemporaneous with sedimentation are examples of synsedimentary phenomena. The term *synsedimentary* also is commonly applied to a particular stage of diagenesis in which there is alteration of sediment contemporaneously or penecontemporaneously with sedimentation (precipitation of sulphides and cementation by carbonate mineral are examples of synsedimentary diagenesis). The term *diagenesis* (and *diagenetic*) refers to the physical, biological, and chemical processes, acting alone or in concert, that overprint sediments after accumulation, and products resulting from these processes. Precipitation of carbonate within sediment to develop indurated layers, for instance, is a diagenetic phenomenon, and the precipitate may be referred to as "diagenetic carbonate", noting that diagenetic carbonate thus is distinct from any sedimentary carbonate material that has been derived from accumulating skeletons ("biogenic carbonate"), or that derived by chemical precipitation. Sediment fabric terms, such as grain-support, mud-support, grainstone and boundstone, are after Dunham (1962).

The term "organic matter" is used in the sediment descriptions in this paper to refer to the range of materials of various particle sizes that are derived from plants. Organic matter ranges from relatively fresh material, to particles in various stages of decomposition (structural and biochemical breakdown, mediated by microbiological and fungal processes) to elemental carbon.

Sediment *versus* soil

The approach in this paper is from a sedimentary perspective, *i.e.*, the materials accumulated in wetlands are sediments and are described from this sedimentary viewpoint. However, to avoid the confusion in the literature between the notions of "sediment" and "soil", a range of terms in relation to materials underlying wetlands are stipulatively defined below. "Sediment" refers to accumulated material that either has formed wholly within the wetland (autochthonous, intrabasinal sediment, *i.e.*, that formed inside the basin), or has been transported into the wetland (allochthonous, extrabasinal sediment, *i.e.*, that formed outside the basin). The term can be applied to individual sediment types or to interlayered deposits. Thus, carbonate mud is a type of wetland sediment, and peat is a type of wetland sediment, since they both form as intrabasinal accumulative deposits. "Sedimentary" refers to any material accumulations that have formed as sediments. "Sedimentary fill" refers to the total aggregate of deposits filling a wetland basin. "Stratigraphic" and "stratigraphy" refer to the accumulated *sequence* of sediments.

"Soil" in this paper refers to the altered material near or at the surface of any pre-existing sediment or rock body that has been biologically, chemically, or physically modified under extant conditions (Buol *et al.*, 1973; Arnold 1983; Jackson 1997), *e.g.*, the weathering of the surface of the Bassendean Sand (Playford & Low 1972) on the Swan Coastal Plain, or the surface weathering of granite. Soils generally are not accretionary but degradational (Hunt 1972), though some authors place in the realm of soil the thin layer of fresh to decomposed organic matter accumulated *above* the mineral material (parent body), designated as the "O horizon", even if it has accreted to several centimetres in thickness (Buol *et al.*, 1973). Soils that have formed under past climatic or hydrologic conditions, and are not therefore extant, are *palaeosols*.

In this context, wetland sediments are the primary accumulates within a wetland basin, and not physical, chemical or biogenic alteration products of pre-existing material, and if soils are developed on them, the wetland soils will be near surface alteration of those primary materials (Fig. 2A). Thus, a wetland basin filled with white carbonate mud is filled with carbonate sediment, and the grey carbonate surface mud layer, say, 10 cm thick, of humified root-structured material at its surface is the wetland soil. Pre-existing Pleistocene quartz sand, *e.g.*, the Bassendean Sand underlying a wetland is the basement material (note: the term "basement" here refers to the floor of the wetland basin and is not to be confused with the notion of basement referring to Precambrian rocks). Where such quartz sand immediately underlies the wetland floor, and there is no development of wetland sediment, the surface grey sandy layer, say, 10 cm thick, of humified root-structured material developed on the sand is the wetland soil.

The term "soil" carries the implication that any layering developed within it (*e.g.*, the A, B and C horizons, or the A1, A2, and K horizons) has developed as a result of internal horizontal partitioning ("horizonation", *cf.* Buol *et al.*, 1973) as a result of leaching, export (removal), or redistribution of materials physically, chemically, and biogenically within the soil profile on a pre-existing parent material. As such, chromatic, compositional or textural "layering" in the soil profile is the result of pedogenic processes, *and the horizontal differentiation therein is interrelated.* Stratigraphic sequences, *e.g.*, interlayered accumulations of diatomaceous mud, biogenically derived organic matter and carbonate mud, are the result of the addition and accumulation of material generated within a basin and from the water column, and are not alterations or modifications of pre-existing materials. These horizontally-oriented differentiations are due to sedimentary accretion under differing regimes of water chemistry, or climate, or biotic assemblages, and are not internally interrelated. As such, the application of the term "soil" to stratigraphically layered material in a wetland accumulated from the intrabasinal processes is not correct.

In contrast to these definitions and concepts outlined above, practitioners in geomorphology, soil science, and wetlands tend to have a wider view of the term "soil", and would use it to refer to all the materials that underlie wetlands, and thus would apply the term to sediments, sedimentary-fill, stratigraphic sequences, and diagenetic products.

Commonly, in wetlands, there is addition of fine-grained wetland sediment (*e.g.*, organic matter, diatom mud, carbonate mud, or mud-sized phyllosilicate minerals) by infiltration or bioturbation *into* any underlying porous basement substrate, such as sand or gravel. This process may result in a "muddy" sand or gravel (Fig. 2B). The fine-grained material is interstitial to the sand or gravel grain-support framework (Dunham 1962), and not merely grain-coating, as is often the case

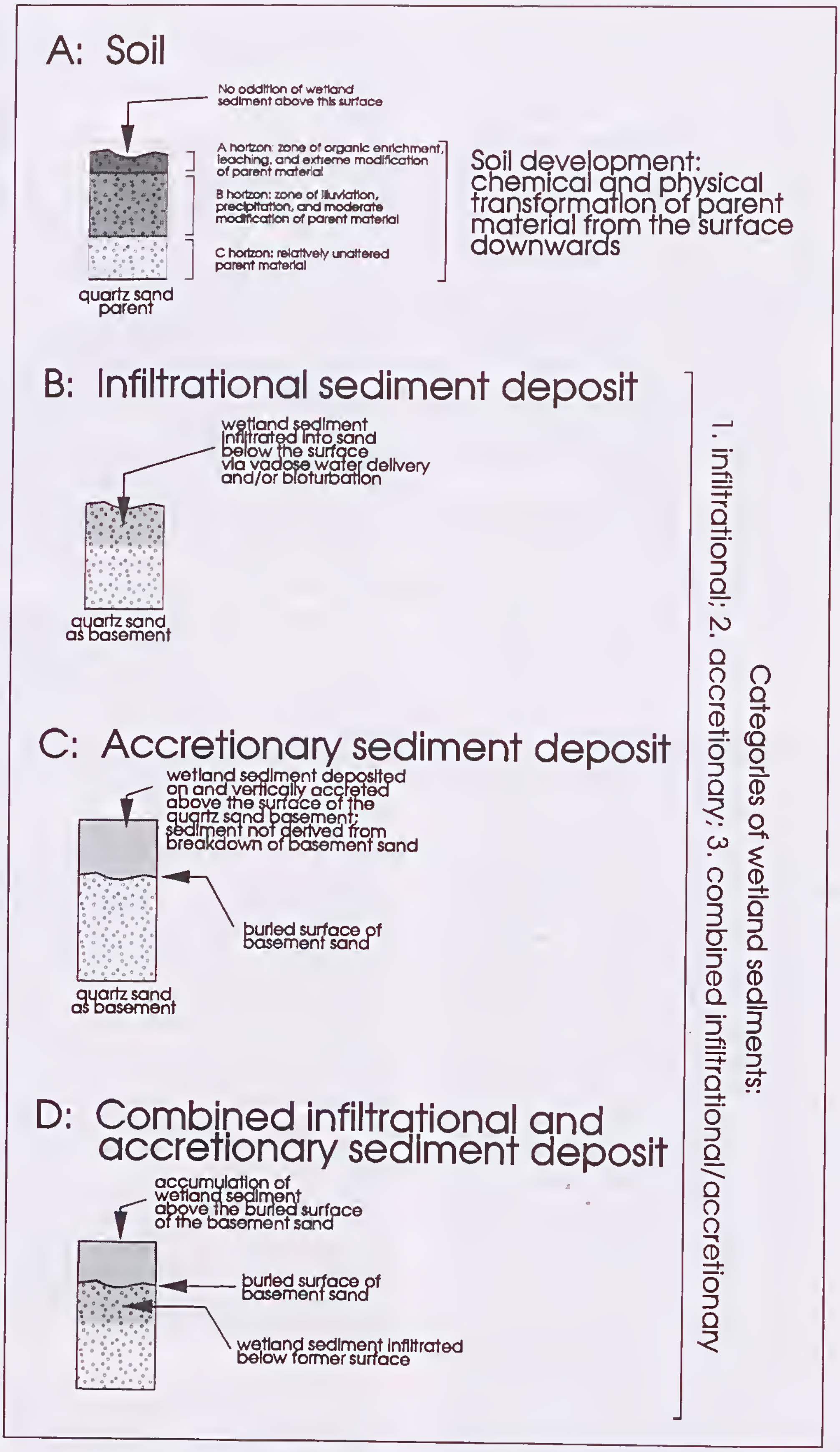

A: Soil
No addition of wetland sediment above this surface
A horizon: zone of organic enrichment, leaching, and extreme modification of parent material
B horizon: zone of illuviation, precipitation, and moderate modification of parent material
C horizon: relatively unaltered parent material
quartz sand parent
Soil development: chemical and physical transformation of parent material from the surface downwards
B: Infiltrational sediment deposit
wetland sediment infiltrated into sand below the surface via vadose water delivery and/or bioturbation
quartz sand as basement
C: Accretionary sediment deposit
wetland sediment deposited on and vertically accreted above the surface of the quartz sand basement; sediment not derived from breakdown of basement sand
buried surface of basement sand
quartz sand as basement
D: Combined infiltrational and accretionary sediment deposit
accumulation of wetland sediment above the buried surface of the basement sand
buried surface of basement sand
wetland sediment infiltrated below former surface
Categories of wetland sediments:
1. infiltrational; 2. accretionary; 3. combined infiltrational/accretionary

Figure 2. Concepts of soil *versus* sediment, as used in this study. A. Soil as a near surface alteration of parent material, using quartz sand as an example. B. Sediment autochthonously formed within a wetland and infiltrated into a porous basement substrate, in this case mud infiltrating the sand.; this type of deposit is *infiltrational* sedimentation. C. Sediment autochthonously formed within a wetland and vertically accreted above a basement substrate, in this case mud overlying sand; this type of deposit is *accretionary* sedimentation. D. Sediment autochthonously formed within a wetland and first infiltrated into a porous basement substrate, and then vertically accreted above a mud-clogged basement substrate.

for humus material in the A horizon of soils. The zone of "muddy" sediment may develop as a material in its own right, immediately underlying the floor of a wetland, or may be a unit that is transitional between any accreted wetland sediment and the basement substrate. The "muddy" material that has formed by infiltration of wetland sediment into underlying basement materials is the product of *infiltrational* sedimentation. Any material that accumulates above the surface of basement materials is the product of *accretionary* sedimentation (Fig. 2C). Both may be present in the one wetland (Fig. 2D). Infiltrational material, accretionary material, and combined infiltrational/accretionary material are treated in this paper as wetland sediment.

The processes leading to the development of wetland soils, and types of wetland sediments on the Swan Coastal Plain are summarised in Figure 3.

Materials and methods

A wide-ranging sediment sampling programme was undertaken at the surface of wetlands, in their stratigraphic sequence, across the width and along the length of the central Swan Coastal Plain in the different geomorphic, hydrologic and hydrochemical settings, in order to fully capture potential variability in these sediments. Samples were collected from hand cores and stratigraphic intervals in transects from some 143 wetlands (Appendix 1). Stratigraphy of wetlands was determined by examination of dewatered trenches and excavations (to 4 m) in 17 wetlands, and shallow augering (to 5 m) in 70 wetlands. Additionally, in 35 of the wetlands, reverse-air-circulation coring to 30 m was undertaken. The cliff faces provided by dewatered trenches and excavations allowed direct observation and description of stratigraphy, sedimentary and biogenic

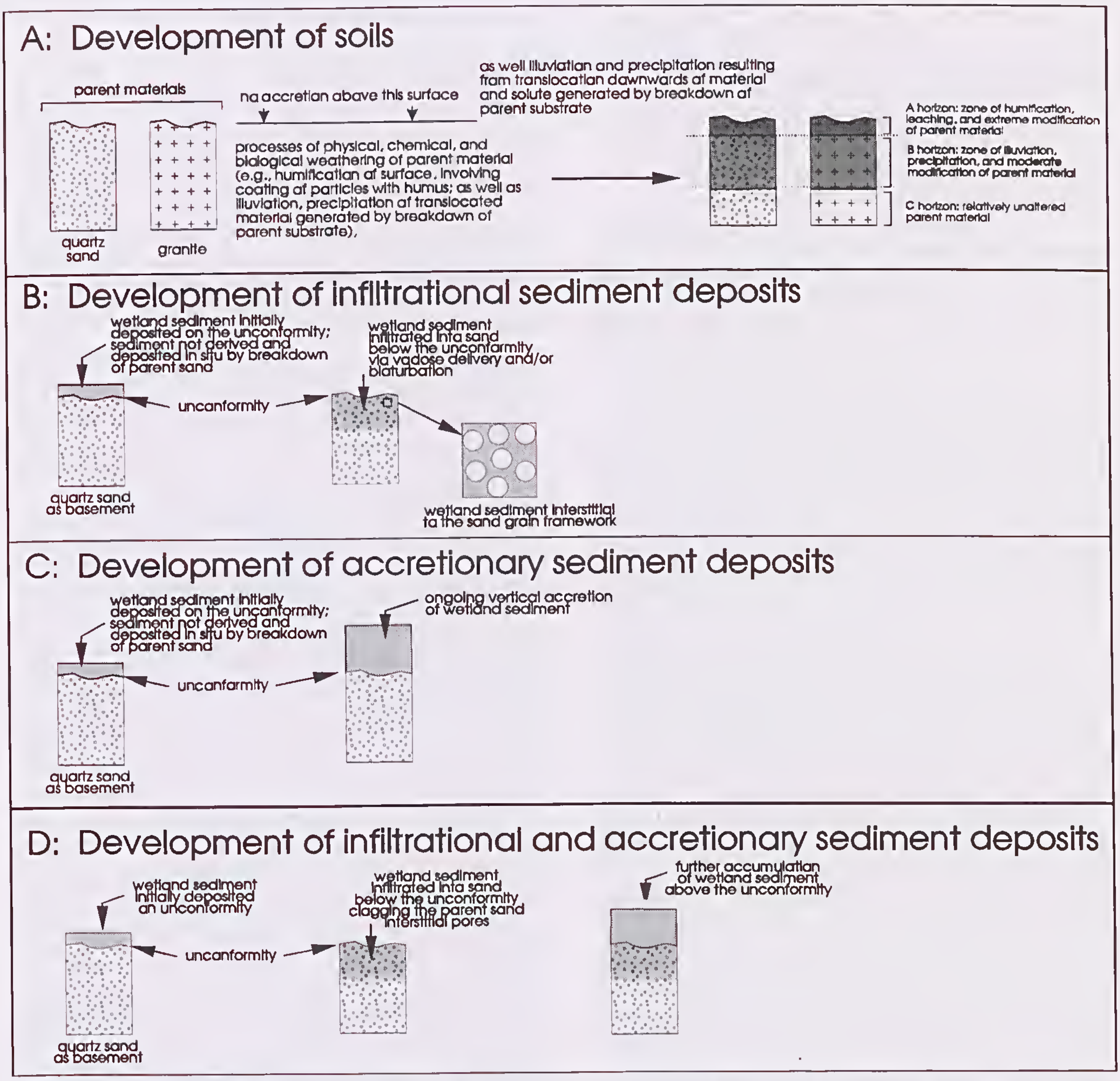

A: Development of soils
parent materials
quartz sand
granite
no accretion above this surface
processes of physical, chemical, and biological weathering of parent material (e.g., humification of surface, involving coating of particles with humus; as well as illuviation, precipitation of translocated material generated by breakdown of parent substrate),
as well illuviation and precipitation resulting from translocation downwards of material and solute generated by breakdown of parent substrate
A horizon: zone of humification, leaching, and extreme modification of parent material
B horizon: zone of illuviation, precipitation, and moderate modification of parent material
C horizon: relatively unaltered parent material
B: Development of infiltrational sediment deposits
wetland sediment initially deposited on the unconformity; sediment not derived and deposited in situ by breakdown of parent sand
unconformity
wetland sediment infiltrated into sand below the unconformity via vadose delivery and/or bioturbation
quartz sand as basement
wetland sediment interstitial to the sand grain framework
C: Development of accretionary sediment deposits
wetland sediment initially deposited on the unconformity; sediment not derived and deposited in situ by breakdown of parent sand
unconformity
ongoing vertical accretion of wetland sediment
quartz sand as basement
D: Development of infiltrational and accretionary sediment deposits
wetland sediment initially deposited on unconformity
unconformity
wetland sediment infiltrated into sand below the unconformity clogging the parent sand interstitial pores
further accumulation of wetland sediment above the unconformity
quartz sand as basement

Figure 3. Processes operating to develop wetland soils and wetland sediment. In (A), quartz sand and granite are used as examples to illustrate the development soils.

structures, and sediment types under wetlands. Artificial exposures were described in 12 un-named wetland basins at Osborne Park, Bullcreek, and Forrestdale, as well as in excavation trenches in Lake Gwelup, Little Carine Swamp, Lake Pinjar, and Karrinyup Road Swamp. Sediments from trenches, excavations, and cores were described in the field in terms of colour, structure, fabric, texture, and composition.

Short cores of *in situ* sediment were obtained from a range of wetlands to study surface and near-surface sedimentary structures and micro-structures. These short cores were obtained by pushing 10 cm diameter PVC pipes, 10–30 cm long, into the substrate, retrieving them, and returning them to the laboratory. At some 30 sites, 75–100 cm long cores also were obtained. In the laboratory, the cores, generally in a water saturated state, or at least with pellicular water, were frozen for storage and ice-hardening. The cores later were longitudinally sliced while frozen to cleanly expose the stratigraphy and sedimentary structures. One half was returned to frozen storage as archive material; the other half was photographed, and used in further analyses.

In the laboratory, the samples of sediment were described and analysed using five progressive levels of detail to provide a comprehensive view of the variety of sediment types.

Firstly, the large range of surface sediments, stratigraphic samples, and hand cores from all the wetland sites, involving several hundred samples, were examined and described as to colour, texture, and composition, and categorised according to their sand and mud content (*i.e.*, clean sand, muddy sand, sandy mud and mud) following the grain-support *versus* mud-support concept of Dunham (1962). With the aid of a stereomicroscope and a light transmitting microscope the presence of carbonate in sand and mud was determined (with dilute HCl), carbonate intraclasts, carbonate skeletal tests and their fragments, plant material (stems, roots, fibres, leaves), quartz sand, quartz silt, lithoclast sand, carbonate mud, invertebrate skeletal debris, and sponge spicules (as monaxons), and mud-sized phyllosilicate minerals were identified, and sediment was assigned to size fraction categories of gravel, or coarse, medium, fine or very fine sand, muddy sand, or mud.

Secondly, examination of sand grain mounts and mud particle mounts, where sand and mud-sized fractions, respectively, are dispersed in a fluid medium on a glass slide (Swift 1971), and thin sections, under a polarising petrographic microscope was undertaken on a selective basis for *c.* 200 samples. Under a petrographic microscope with high power for resolving mud-sized particles, grains in the sand and mud particle mounts were categorised in types based on their size and shape, and their crystallinity and mineralogy determined on their colour, refractive index, cleavage, and birefringence (Kerr 1959). With this method, very fine-grained plant remains, diatoms and their fragments, various types of siliceous monaxon sponge spicules (megascleres, microscleres, and gemmoscleres; *cf.* Williams 1980), siliceous phytoliths (Meunier & Fabrice 2001), and various invertebrate skeletons (*cf.* Williams 1980), in addition to the grains noted above, were identified. Thin section study of epoxy-impregnated sediments, and of any hard layers in the wetlands was undertaken under a petrographic microscope for about 100 selected samples.

Thirdly, the content of organic matter and calcium carbonate in a range of black, dark grey, and brown sediments was determined in some 100 samples using a variety of peats, peaty sediments, and dark grey fine-grained sediments – the problem of determining organic matter content was not an issue for carbonate-mud-dominated sediments or diatomite-dominated-sediments. The samples were divided in three sets of subsamples. One set was processed by combustion at 550° C and then at 1100° C. Another set was prepared as mud particle mounts for examination under a petrographic microscope. The third set was processed by acid digestion (using dilute HCl) to estimate the content of $CaCO_3$. Since loss of weight on ignition at 550° C can be due to loss of organic carbon, loss of sulphur liberated as SO_2 from sulphides (if sulphide was present in the sediment), and other volatiles liberated from the combusting organic matter, it may not be a direct measure of the content of organic carbon or even organic matter. Additionally, the loss of weight on ignition at 1100° C may not be a direct measure of primary $CaCO_3$ content since some $CaCO_3$ could have been generated from organic matter rich sediments during their combustion at 550° C. Hence, some independent calibration of sediment composition was undertaken for organic-matter rich sediments and dark grey sediments. This involved the point counting procedure, and chemical analyses, mentioned above. Mud particle mounts were point-counted under a petrographic microscope to estimate their content of organic matter, carbonate, quartz silt, diatoms, sponge spicules, and phytoliths, and the data compared to the results from the combustions to assess within the sample the amount of organic matter, biogenic silica, and carbonate mud. After combustion, opportunity also was taken to examine the ash as grain mounts and mud particle mounts under a petrographic microscope as these residues commonly are comprised of the concentrated remains of biogenic silica. Fifty selected pre-combustion samples and their combustion residues were analysed by mass spectrometry (using ICP-MS) and XRD to determine their elemental nature (Na, K, Ca, Mg, Fe, As, Cd, Pb, S and Si) and mineralogy (carbonate minerals, quartz, biogenic silica, pyrite, marcasite, arsenopyrites, goethite, haematite), respectively, as a record of wetland sediment geochemistry. The results of the content of Fe and S, and their correlation, also provided another internal assessment of the contribution of sulphide minerals to loss on ignition at 550° C.

Fourthly, more detailed systematic analyses were undertaken for some 32 selected samples obtained from various locations and depths for the purpose of typifying a range of muddy sediment types, and particularly muds, sandy muds, and muddy sands. In this paper, these samples are referred to as the "wetland sediment standards". These analyses involved all the procedures outlined above as well as sieving to quantitatively determine sand *versus* mud content, acid digestion and furnace combustion to determine the content of carbonate and organic matter, respectively, of the mud and sand fractions, X-ray diffractometry (XRD) to determine mud fraction mineralogy, and routine photography and description of sand and mud fractions under a stereoscopic binocular microscope and petrographic microscope.

Fifthly, scanning electron microscopy (SEM), and associated analyses, were undertaken for a subset of the 32 wetland sediment standards and 30 other sediments to determine the crystal form and characteristics of the fine-grained constituents to ascertain their ultrastructure and hence their origin, and to confirm the nature of the silt-sized and clay-sized opaline silica and amorphous silica from their X-ray diffractometry patterns. During the SEM, images of fields of view 100–200 µm in size were obtained using back-scattered electron emissions (BSE) in order firstly to map the distribution of average atomic number, which was used as a surrogate to determine the consistency of element distribution, and hence consistency of the distribution of particle types, and also to map the distribution of selected elements (specifically C, Ca, Mg, Al, and Si as indicators of organic matter, calcite/aragonite, Mg-calcite, phyllosilicate minerals, quartz, and diatoms, respectively). This provided a method for evaluating the homogeneity, for instance, of the carbon content of peat, or the diatom content of diatom-bearing peat. Additionally, routine spot analyses of 5 to 6 particles within each SEM field of view, some 100–200 µm across, with particle selection based on the heterogeneity of the SEM image, or heterogeneity of the BSE field, or on particle shape, were undertaken using Energy Dispersive Spectroscopy (EDS), which allowed for determination of relative element content of individual particles. With this method, elemental content of particles, combined with information on their shape, allowed identification of diatoms, very fine and ultrafine-grained diatom fragments, sponge spicules, invertebrate skeletons/tests and their fragments, quartz silt, mud-sized phyllosilicate minerals, organic carbon, plant detritus, calcite, and framboidal pyrite.

To assist with identification of particle sizes < 63 mm in size under SEM, standards of several mollusc species, ostracods, and *Chara* species and other carbonate-impregnated filamentous algal species were prepared for XRD and SEM analyses. The XRD analyses provided data on the range of mineralogic types that comprise skeletal grains, information particularly useful in interpreting the origin of mud-sized carbonate particles. The SEM and associated EDS analyses of known skeletal grains provided micromorphologic, microstructural, and ultrastructural standards for comparisons with wetland sediment particles, and provided information for the various mollusc species, crustaceans, and *Chara* on the range of their composition in terms of calcite and aragonite content, their Mg content in low Mg calcite and high Mg calcite, and in terms of Mg, Sr and Pb content in aragonite cements.

In the field, during appropriate seasons, various large-scale and small-scale physical and biological processes, instrumental in developing sediment types, were observed within and adjacent to wetlands. These processes, such as wave action, sheet wash, bioturbation by fauna, and desiccation, provided information on some of the mechanisms of sediment particle generation, and the development of sedimentary structures and sediment types.

Regional geologic and geomorphic setting

The Swan Coastal Plain is the Quaternary surface of the Perth Basin (Playford *et al.*, 1976). The Plain comprises distinct large-scale landforms which are either arranged subparallel to the Darling Scarp or the coast, or are associated with major rivers. These landforms correspond to the main sedimentary formations in the region (Woolnough 1920; McArthur & Bettenay 1960; Playford *et al.*, 1976; McArthur & Bartle 1980a,b; Semeniuk & Glassford 1987, 1989; C A Semeniuk 1988; Semeniuk *et al.*, 1989; Geological Survey of Western Australia 1990; Semeniuk 1995):

- Pinjarra Plain: flat to gently undulating alluvial fans fronting the Darling Scarp and Darling Plateau (underlain by sand, laterite, and the Precambrian rocks), as well as floodplains and various sized channels; underlain by the Guildford Formation (clay, laterite, sand, muddy sand);
- Bassendean Dunes: undulating terrain of low degraded dunes (varying in relative relief from 20 m to almost flat), and interdune flats and basins; underlain by the Bassendean Sand (quartz sand) of Pleistocene age;
- Spearwood Dunes and Yalgorup Plain: large-scale, linear, near-continuous subparallel ridges (*c* 60m relief) and intervening narrow and steep-sided depressions, or narrow plains; underlain by Pleistocene limestone (aeolianite and marine limestone) blanketed by quartz sand;
- Quindalup Dunes: Holocene coastal quartzo-calcareous sand dunes, beach ridge plains, tombolos and cuspate forelands.

The units relevant to this paper are the Bassendean Dunes, which are ergs formed during glacial periods, the Spearwood Dunes, which were composite ergs, *i.e.*, quartz sand desert ergs formed during glacial periods, and calcareous coastal ergs formed during interglacial periods (Semeniuk & Glassford 1988; Glassford & Semeniuk 1990), and the Pinjarra Plain. In these settings, there are two main lithologic/stratigraphic units that either adjoin or underlie wetlands: 1. Pleistocene quartz sand, and 2. Pleistocene limestones.

Pleistocene quartz sand is typically yellow, but varies from white to orange to locally red. Yellow sand forms thick formations landward of Pleistocene limestones on the coastal plain, but extends as sheets covering these limestones, along unconformities within the limestone, and underlies the coastal limestones (Allen 1981). The yellow sand is mostly homogeneous, but locally there is large-scale, aeolian cross-layering (Glassford & Semeniuk 1990). Towards the contact with Pleistocene aeolian limestones to the west, the yellow sand contains scattered limestone lenses (Semeniuk & Glassford 1988). Yellow sand is typically composed of quartz, with moderate to trace amounts of feldspar, and minor kaolin, goethite, and heavy minerals (Prider 1948; Glassford & Killigrew 1976; Glassford 1980). Yellow quartz sand grains have a thin coating of kaolinite clay and quartz silt impregnated with goethite (yellow) and/or haematite (red) (Glassford 1980). Goethite-pigmented kaolinite and quartz also comprise the < 90 µm fine-grained interstitial material to yellow sand (Glassford 1980).

Pleistocene limestones in near-surface sections mostly are composed of an overlapping series of aeolianites, with local lenses, wedges and thin sheets of intercalated marine units. These limestones have been referred to the Tamala Limestone, the Tims Thicket Limestone, the Kooallup Limestone, and the Peppermint Grove Limestone (Playford *et al.*, 1976; Semeniuk & Johnson, 1982, 1985; Searle & Semeniuk, 1985; Semeniuk 1995). The aeolianites are large-scale cross-layered, mainly medium sand-sized quartz, skeletal lithoclastic grainstone, cemented by sparry calcite and micritic calcite (locally forming calcrete). Limestone surfaces are mantled by yellow quartz sand, penetrated by pipes filled with yellow sand, and dissected by karst features.

Wetlands on the Swan Coastal Plain

A wide range of basin wetland types occur on the Swan Coastal Plain, varying in size, shape, water characteristics, stratigraphy and vegetation (Semeniuk 1988; Semeniuk *et al.*, 1990). Dependent on setting, wetlands can range from large linear lakes to small, round or irregular, seasonally damp wetland basins; from fresh water to hyposaline (brackish) to saline; from basins which perch surface water to those which are recharged by groundwater; with vegetation cover which can vary from herbland to forest. These attributes are determined by regional features such as geology, geomorphology, soils, climate and hydrology, and local physical/ chemical processes such as groundwater flow and karstification. While there is a large variety of wetland types across the Swan Coastal Plain, using criteria of size, shape, patterns of clustering, water quality, substrates, and maintenance processes, they can be aggregated into natural groupings that are termed consanguineous suites (Semeniuk 1988).

In this paper, the wetlands for sediment study have been drawn from the following consanguineous suites: 1. Yanchep Suite, 2. Balcatta Suite, 3. Coogee Suite, 4. Stakehill Suite, 5. Bibra Suite, 6. Jandakot Suite, 7. Riverdale Suite, 8. Gnangara Suite, 9. Mungala Suite, and 10. Bennett Brook Suite (Semeniuk 1988). Site descriptions of these settings and a description of the wetlands from which the 32 sediments were studied in more detail are provided in Appendix 2.

Types of sediment fills

Sedimentary particles

A variety of particles comprise wetland sediments, ranging from those that are biogenic, siliciclastic, to abiotic intraformationally-generated. Biogenic particles include whole shells, frustules, tests, and skeletons (*e.g.*, molluscs, diatoms), disintegrated remains of biota (*e.g.*, diatoms, charophytes), to decayed plant remains and detritus. There is a large range of organisms that inhabit wetlands of the Swan Coastal Plain (Hembree & George 1978; John 1981, 1993; Balla & Davis 1993; Davis *et al.*, 1993; Helleren & John 1994; Maly *et al.*, 1997; Chessman *et al.*, 2002), and in the arena of invertebrates and microscopic plants, many make conspicuous and/or significant contributions to the wetland sediments as skeletal remains (*e.g.*, the calcareous remains of molluscs and ostracods, the siliceous remains of freshwater sponges, the siliceous remains of diatoms, and siliceous phytoliths). There also are other organic particles that contribute mainly to the surface sediments of wetlands; *e.g.*, the chitonous tests of insects. However, while some of these latter biogenic particles can occur in the shallow stratigraphic sequences, many of the exoskeletons of invertebrate fauna, such as chitonous tests, do not survive synsedimentary diagenesis or shallow burial diagenesis. Only particles that are preserved in the sedimentary record have been described here.

XRD and EDS of shelly biota and *Chara* and carbonate-impregnated filamentous algae show the following: molluscs, depending on species, may be wholly calcitic, or Mg-calcitic, or interlayered aragonitic and calcitic (similar to the mineralogy of marine molluscs; *cf* Bathurst 1971); ostacods are calcitic, or aragonitic and calcitic; *Chara* may be calcitic, Mg-calcitic, or aragonitic; and that carbonate-impregnated filamentous algae have mediated precipitation of calcite or Mg-calcite as crusts on their cell walls. The implications are that carbonate sediments composed of, or derived from these biota will have a similar range in mineralogy.

Grains of pollen, spores, phytoliths, and microcharcoal (Clarke 1988; Faegri *et al.*, 1989; Odgaard 1992; Meunier & Colin 2001) also occur in wetland sediments, and are important in the analyses of sediments and stratigraphic sequences for palaeo-environmental studies and palaeoclimatic reconstructions. However, while their occurrence is noted, they do not contribute enough material to the sediments to be recognised as distinct wetland sediment types.

A note is made here on the use of the terms "clay mineral", "phyllosilicate", and "phyllosilicate clay" for particles that comprise the fine-grained component of many wetland sediments. The term "clay" has two meanings in the Earth Sciences (Jackson 1997). One has a grainsize connotation denoting particles < 4 µm. The other is as a rather imprecise mineralogical term, *viz.*, "clay mineral", intended to cover categories of layered silicates (hence "phyllosilicate clay") such as kaolinite, smectite, illite, halloysite, and montmorillonite (Kerr, 1959; Sinkankas 1964; FitzPatrick 1983), based on an assumption that it is finely crystalline layered silicates that dominantly comprise "clay-sized" minerals. However, as described later, calcite, quartz, goethite, and feldspar can occur as clay-sized particles, but they are not viewed traditionally as "clay minerals", and hence the term "clay mineral" is not appropriate for use in this paper. The range in grainsize of kaolinite further complicates the use of the term "clay mineral" because in the wetland sediments of this study kaolinite manifests a variety of grainsizes: it can be very fine (< 1 µm), and hence conforming with the notion of being a "clay-sized" mineral, but can range up to medium silt size. Additionally, some micas, such as muscovite, can be comminuted to silt or clay-sized and hence occur in the < 63 µm fraction. Given these problems, the term "clay mineral" is not used in this paper, and while the term "phyllosilicate" is used to refer to the mineral group of layered silicates, it is not used in association with "clay" as it is often traditionally used. Kaolinite, white mica (muscovite), hydrobiotite, and montmorillonite, occurring in wetlands sediments, are referred to as

Table 1

Particle types in wetland sediments

mud-size particles (< 63 µm in size)

organic mud-sized particles < 63 µm, and mostly < 4 µm in size;
microcharcoal < 63 µm in size;
carbonate mud particles (calcite, Mg-calcite, aragonite, dolomite), < 63 µm in size, mostly < 4 µm in size, as comminuted shell, intraclasts, and charophytes, single crystals, and undifferentiated types;
quartz silt particles, < 63 µm in size;
phytoliths as silt-sized and clay-sized siliceous particles, < 63 µm in size;
diatom as silt-sized and clay-sized particles, < 63 µm in size;
sponge spicule fragments, < 63 µm in size;
phyllosilicate mineral particles (kaolin, montmorillonite, white mica), < 63 µm in size, mostly < 4 µm in size;
goethite mud, < 4 µm in size;
feldspar silt, < 63 µm in size;
heavy minerals (*e.g.*, haematite, rutile), < 63 µm in size (mainly silt).

sand-size particles (63 µm – 2000 µm in size)

quartz sand, mostly 125 µm to 1000 µm in size;
carbonate intraclast sand, mostly 125 µm to 2000 µm in size;
sponge spicules, mostly 100 µm to 300 µm in size;
diatom intraclast sand, mostly 125 µm to 2000 µm in size;
peat clast sand, mostly 125 µm to 2000 µm in size;
microcharcoal and charcoal 63 µm to 2000 µm in size;
carbonate shell-fragment sand, mostly 125 µm to 2000 µm in size;
heavy minerals (*e.g.*, haematite, rutile), mostly 63–125 µm in size;
gypsum crystals as single crystals and rosettes, mostly 63–250 µm in size.

gravel-sized particles (> 2000 µm in size)

carbonate intraclast gravel particles, > 2000 µm in size;
carbonate shell (gastropod) gravel, > 2000 µm in size;
diatom intraclast gravel, > 2000 µm in size;
peat intraclast gravel, > 2000 µm in size;
charcoal > 2000 µm in size.

Vegetation material

plant fibres, detritus, leaves, flowers, fruit, twigs, branches and trunks

"mud-sized phyllosilicate minerals" or as "mud-sized phyllosilicate mineral particles" to circumvent the issue that these "clay minerals" can range from clay-sized to silt-sized. Sediments composed dominantly of kaolinite are termed "kaolinitic mud" since there will be clay-sized and silt-sized kaolinite therein.

The main sedimentary particles and sedimentary components that constitute wetland sedimentary fill are shown in Table 1. The methods of identifying these sedimentary constituents in wetland sediments in this study are summarised in Table 2.

Current terms for wetland sediment types formed from the common particles

In the literature, there are a number of terms that apply to deposits formed in wetlands that are relevant to the particle types encountered in this study, *viz.*, those composed of organic (plant) matter, diatom remains, sponge material, fine-grained carbonate mud, or water saturated sand. Sediments composed of organic matter, mostly as decayed plant material, have been termed organic mud or organic ooze, sapropel to saprocol, and peat. The terms "organic mud", "organic ooze", "muck", or "gyttja" could be applied generally to deposits that are mud-sized and composed of organic carbon and decayed plant remains, but are more relevant to the immediate surface layers of organic deposits in wetlands where sediments have a degree of thixotrophy than to the more consolidated deposits at shallow to moderate depths. "Sapropel" is a term for unconsolidated jelly-like ooze or sludge composed of plant remains macerating and putrefying on the shallow bottoms of lakes and seas, and "saprocol" refers to an indurated sapropel (Jackson 1997). The terms are part of a sapropelitic series that reflect increasing consolidation into coal (*viz.*, sapropel, as organic ooze, saprocol, as indurated sapropel, and saprodil, as sapropelitic coal of Tertiary age, saprodite, and so on). In the soil literature, materials composed of accumulated organic matter (or peat) are referred to as "histosols", an order of soils (USDA 1975; FitzPatrick 1983), with further subdivision into suborders based either on the degree of decomposition, *e.g.*, "fibrist" (the least decomposed), "hemist" and "saprist" (the most decomposed), with the extent of decomposition assessed by the content of plant fibre (Soil Survey Staff 1998), or on moisture content. In the Earth Sciences, unconsolidated deposits of semi-carbonized plant remains in a water-saturated environment are referred to

Table 2

Method of identification of particle types

Mud-size particles (< 63 µm in size)	**Method of identification**
organic mud-sized particles carbonate mud particles quartz silt particles sponge spicule fragments phytoliths diatom silt and clay particles phyllosilicate mineral particles goethite mud feldspar silt microcharcoal	dealing only with the < 63 µm size class separated by sieving: combustion for organic matter; SEM and EDS; acid-digestion, and XRD, SEM and EDS for carbonate particles; SEM and EDS and light microscopy for diatoms and types of carbonate mud particles; XRD and EDS for phyllosilicate mineral particles, goethite mud and feldspar silt; high resolution petrographic microscopy for plant remains, quartz, phyllosilicate mineral particles, diatoms, phytoliths, carbonate particles, and sponge spicules.
Sand-size particles (63 µm – 2000 µm in size)	
quartz sand sponge spicules carbonate intraclast sand peat intraclast sand carbonate shell-fragment sand microcharcoal and charcoal gypsum crystals	binocular microscopy and petrographic microscopy for the quartz sand and gypsum, sponge spicules, and carbonate sand types; binocular microscopy for the peat clasts.
Gravel-sized particles (> 2000 µm in size)	
carbonate intraclast gravel carbonate shell (gastropod) gravel diatom intraclast gravel peat intraclast gravel charcoal	binocular microscopy for the peat, diatomite, and carbonate clasts; light microscopy for diatoms within clasts.
Vegetation material	
plant fibres, detritus, leaves, flowers, fruit, roots, rhizomes, culms, twigs, branches and trunks	visual inspection on excavation faces, and sieve residues, and binocular microscopy.

as "peat" (Jackson 1997). Teakle & Southern (1937) use two terms to refer to deposits (or "soils") of organic material: peat, and muck. Following Dachnowski (1920), Teakle & Southern (1937) recognised three main groups of peaty material: sedimentary or pulpy peat, fibrous peat, and woody peat. For purposes of this paper, the single term "peat" will be used for surface and subsurface sedimentary deposits composed of plant debris, plant detritus, and organic matter, in that it is a term that encompasses organic deposits that range from "ooze" to semi-consolidated material in the sense of Clymo (1983), and with varying structure, fabric and texture (from structureless, laminated, root-structured, to bioturbated, and from fibrous to massive).

Sediments composed mainly of diatoms and their fragments are "diatomite", which is synonymous with the term "diatomaceous earth" (Jackson 1997). The term "diatomaceous earth" carries with it a connotation of the sediment being porous (the result of interstitial porosity developed by platey diatom grains in randomised array in a grain-support framework, as well as intrafrustule porosity), and having low bulk density. It is this interstitial and intrafrustule porosity within "diatomaceous earth" that renders it useful as a filter for industrial and domestic purposes. However, as will be described later, diatoms comprising wetland sediments range from whole to totally fragmented frustules, and as a result, diatomaceous sediments can vary from those with properties close to "diatomaceous earth," to those composed of closely packed fine-grained silica fragments (giving broad XRD peaks typical of diatoms) with the sediment having the properties and bulk density of quartz silt. Given this range of sediment particle possibilities, the term preferred in this paper is "diatomite".

Sediments composed mainly of sponge spicules and fragments are "spongolites" (Jackson 1997). Spongolitic is used herein to refer to wetland sediments with moderate amounts of sponge spicules. There is no current term for sediments composed dominantly of phytoliths, and in this study phytoliths were not of sufficient abundance to warrant coining a lithologic term to cover this category. Phytolithic is used herein to refer to wetland sediments with moderate amounts of phytoliths and fragments.

Sediments composed of fine-grained mud-sized calcium carbonate particles have been termed "carbonate mud", or "calcilutite" (the Latin equivalent for "calcium carbonate mud"). The term "calcilutite" has had a complex and varied history. Originally introduced by Grabau (1903) to refer to limestone composed of mud-sized calcite, the meaning of the term has since expanded to encompass fine-grained limestones, consolidated calcareous mud, and unconsolidated calcareous mud (Bathurst 1971; Jackson 1997), and from an original concept involving only calcitic mud, the term now also has broadened in meaning to include aragonitic mud (Bathurst 1971). In Western Australia, the term "calcilutite" has been used to refer to formations (*e.g.*, the Bridport Calcilutite of Semeniuk & Searle 1987) as well as consolidated earlier Holocene carbonate deposits (Backhouse 1993). In this paper, conforming with the now broadened usage, addressing the issue that carbonate mud in wetlands of the Swan Coastal Plain can grade mineralogically from calcite-dominated to aragonite-dominated, and in recognition that the majority of mud deposits are calcitic or low Mg calcitic, the term "calcilutite" is used to refer to all carbonate deposits, whether consolidated, semi-consolidated, or unconsolidated, and whether the mud-sized particles comprising the calcilutite are wholly calcitic, or dominantly aragonitic, or mixtures of calcite and aragonite.

In the literature, water-saturated sand has been referred to as "gley", or "gleysol", a term in soil science referring to any water-saturated unconsolidated material (FitzPatrick 1983; FAO UNESCO 1974; USDA 1975; Jackson 1997), particularly if it is anoxic. The original term "gley" was a Russian local name for a "mucky soil mass", to connote water-saturated conditions, but has since been redefined in the Soil Sciences to denote sand or soils that are water saturated, in the reduced state (ferrous ion) and grey-green, but with ferric mottles, and within a zone of fluctuating water table (Hunt 1972, Etherington 1983, Mitsch & Gosselink 1986, Sprecher 2001). However, within the Soil Sciences, there is no connotation as to whether the water-saturated sand is a transported sediment or *in situ* soil, as the term can be applied to both settings. The term "gley" is not used in this paper to denote water-saturated sands because of this imprecision, and because the amount of water saturation of wetland sedimentary fill is not relevant to defining and describing wetland sedimentary material. Where quartz sand comprises sedimentary fill as an accretionary sedimentary deposit, it is referred to as "quartz sand". Where quartz sand comprises the Pleistocene basement substrate under the wetland fill sequence, it is referred to as quartz sand basement.

Sediment types, this paper

Ten main end-member sediment types occur in wetlands on the Swan Coastal Plain; they are: 1. peat, 2. peat intraclast gravel and sand, 3. calcilutite (carbonate mud), 4. carbonate skeletal gravel and sand, 5. carbonate intraclast gravel and sand, 6. diatomite, 7. diatomite intraclast gravel and sand, 8. kaolinitic mud, 9. quartz sand, and 10. quartz silt. Mixtures of these end-member sediment types also occur, as will be described later. While sponge spicules are a common component of wetland sediments, occurring within peat and diatomites, generally they do not form "spongolites". Usually, where they occur, sponge spicules and fragments may constitute up to 10% of a wetland sediment, and in this context, the term "spongolitic" `is used as a descriptor to the main wetland sediment name. The main sediments that are spicule-bearing are peats and diatomites, hence there are "spongolitic peat" and

Table 3

Description of the various types of sedimentary structures

Structure	Description/definition
layered	sediment with conspicuous layering evident on > 1 cm scale; often sediment is lithologically interlayered
laminated	sediment with conspicuous lamination evident on < 1 cm, and usually < 1 mm scale; lamination can vary from regular and even, to wavey and uneven
wispy laminated	sediment with discontinuous lamination, with individual laminae occurring as thin wisps; often the lamination is accentuated by compositional differences
homogeneous or structureless	sediment shows no structure and appears texturally and compositionally massive
fibrous	prominent structure imparted by random orientation to vertical orientation of plant fibres, roots, and (decayed) stems
root-structured	prominent structure imparted by ramifying roots
burrow-structured	prominent structure imparted by vertical burrows, where individual burrows are discernible
burrow-mottled	prominent structure imparted by burrows, where individual burrows, though overlapping, are still discernible and impart a colour or texture mottled appearance to the sediment
bioturbated	where abundant, and overprinting earlier phases of biological imprints, root-structuring, or burrowing has proceeded to the extent that individual root-structures and burrow-structures are not discernible, or only vaguely discernible, and there is an overall mottled appearance in the sediment
texture-mottled	where mottling is distinguished by textural differences, *e.g.*, sand mottles in mud
colour-mottled	where mottling is distinguished by colour differences
fenestral	small flattened cavities, usually parallel to layering, and developed in cemented carbonate intraclast sediment; fenestrae are *c.* 1 mm up to 1 cm in size (*cf.* Tebbutt *et al.*, 1965; Jackson 1997)
vesicular	small open structures produced by bubbles of air or other gases; usually a few millimetres up to 1 cm in size
brecciated	sediment exhibiting a fragmented structure, formed by desiccation and cracking at centimetre to metre scale

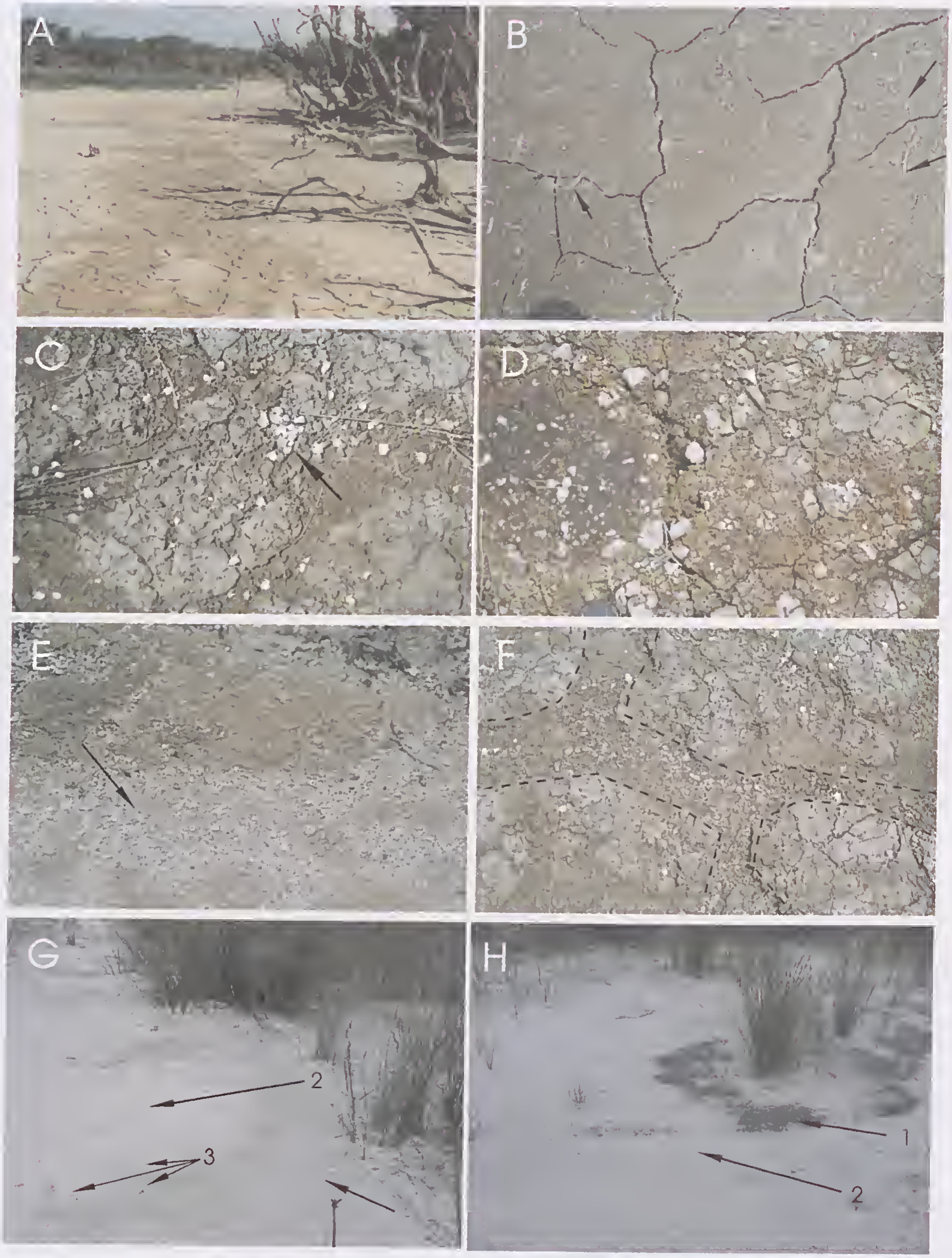


Figure 4. Sediments and sedimentary features from various wetlands. A. Desiccation of calcilutite forming mud crack polygons at the surface of the wetland margin during a dry phase in the hydrological cycle. B. Desiccation of diatomite forming mud crack polygons at the surface of the wetland margin during a dry phase in the hydrological cycle. Some examples of diatom mud-coated vegetation debris (twigs) are arrowed. C. Development of intraclast gravel of diatomite along a wetland margin by break-up of desiccated diatomite; older bleached diatomite intraclasts are arrowed. D. Surface layer of sediment showing several cycles of diatomite intraclasts (medium grey to bleached) incorporated into the sediment. E. Small thin lens of intraclast gravel of diatomite (arrowed) concentrated by wave action during high water. F. Concentration of diatomite intraclast gravel in a polygonal desiccation crack (outlined). G. Diatomite intraclasts (arrow 3) incorporated into the white sand apron (arrow 2) along the edge of a wetland; in this example, the thin sand deposit rests on grey diatomite (arrow 1). H. Thin veneers of white sand (arrow 2) transported into the margin of a wetland by sheet wash, forming an apron, in this example resting on dark grey diatomite (arrow 1).

"spongolitic diatomite". Similarly, peat may contain a significant proportion of diatoms and their fragments, and these sediments are termed "diatomaceous peat". Mixtures of peat, sponge spicules and diatoms are referred to as spongolitic diatomaceous peat.

To complete the picture of the variability and occurrence of wetland sediments of the central Swan Coastal Plain, it is worthwhile to note that within the Quindalup Dunes calcilutite, peat, carbonate muddy sand (to be discussed later), and quartzo-calcareous sand occur as sediment types in the Becher Suite (Semeniuk 2005), calcilutite, peat, carbonate muddy sand, intraclast gravel and sand, and stromatolitic boundstone occur at Lake Walyungup, Lake Cooloongup and Lake Richmond of the Cooloongup Suite, and calcilutite, peat, carbonate muddy sand, and quartzo-carbonate sand occur in the Peelhurst Suite (Semeniuk 1988).

The wetland sediments are described below in terms of: colour; structure (layered, laminated, wispy laminated, homogeneous or structureless, root-structured, burrow-structured, bioturbated, texture-mottled, colour-mottled, fenestral, bubble-structured or vesicular, brecciated; see Table 3); fabric (grain-support, mud-support; *cf.* Dunham 1962); texture (grainsizes of gravel, grades of sand, and mud); and composition (quartz sand, kaolinitic clay, iron oxides, carbonate mud or sand, skeletons, and opaline silica and X-ray amorphous siliceous frustules and skeletons). Some of the field settings of wetland sediments are shown and described in Figure 4. Annotated selected cores of sediments showing overall lithologic appearance and structure are shown in Figure 5. Selected photomicrographs of sediment dispersed on slides, and of SEM images are presented and described in Figures 6–11. The geographic, geomorphic and consanguineous setting of the 32 wetland sediment standards, and the results of detailed microscopy and analyses of these sediments, in terms of sand *versus* mud content, organic carbon content and carbonate content of the mud fraction, and the mineral composition of the mud determined by XRD, are provided in Appendices 2 & 3.

Peat

Peat is a black to grey, and in certain horizons, brown sediment. It is mainly homogeneous to root-structured, and in upper near-surface layers weakly laminated to compositionally layered, to fibrous; some layers at depth in peat profiles also are laminated. Texturally, peat consists of fine-grained organic matter < 63 µm in size, and larger root fibres, stem fibres, plant detritus particles and scattered (< 5%) quartz sand and quartz silt. Local deposits may contain minor amounts of freshwater snails, or their comminuted fragments. There is also a presence of fine-grained iron sulphide (evident as pyrite framboids in SEM, and detected as pyrite and marcasite in XRD), and occurrence locally of arsenopyrites. Cores through peat show an upper layer of partly decomposed leaves, stems, twigs, and roots that grades down within 30 cm, and locally within 100 cm, into fine-grained to fibrous organic material that has scattered plant material, and non-fibrous organic matter. In some peats, at depth, branches, twigs, and logs are still preserved in the fine-grained organic accumulation. Near the surface, root holes and burrows may have oxidation haloes surrounding them. The surface of peats that dry out are polygonally cracked, with desiccation cracks descending locally down to 20 cm into the peat.

In the upper parts of peat, within 10–30 cm of the surface, where the plant material is not wholly decayed, various types of vegetation contributing to the deposit can be recognised, *e.g.*, the leaves of *Melaleuca rhaphiophylla* and *M. cuticularis*, and the leaves, stems and rhizomes of *Baumea articulata* and *Typha* spp (Fig. 5A–C). Roots and plant fibres are also common in these upper layers. Grain-mount microscopy and SEM show peat to be composed of plant detritus in various stages of fungal and bacterially induced structural breakdown (Fig. 8). For instance, large particles are riddled with fungal hyphae.

SEM and petrographic microscopy of many homogeneous or structureless, fine-grained, black to dark grey peat-like materials show them also to have a significant component of diatoms and/or sponge spicules, and siliceous phytoliths. Where diatoms and sponge spicules are abundant, the peats become diatomaceous or spongolitic peat. Sponge spicules and diatoms in peat range from complete spicules and frustules to largely fragmented particles.

Since peat can grade into organic matter rich diatomite and organic matter rich calcilutite, the lithological boundary of peat is set at > 75% content of organic matter (as dry weight), and sediments containing 74%–50% organic matter mixed with diatoms, or calcilutite, are termed diatomaceous peat and calcilutaceous peat respectively (see later). The content of organic matter as dry weight in some typical peats is presented in Table 4.

Multiple values of organic matter content reflect variablity of peat composition spatially, where samples have been collected at a number of sites within a large wetland, or from several proximally located small wetlands within the same consanguineous suite, or collected stratigraphically at the one site.

Peat intraclast gravel and sand

Peat intraclast gravel and sand are a black to grey coarse-grained suite of sediments, ranging from breccias,

Table 4

Content of organic matter in some typical peats on the Swan Coastal Plain (for co-ordinates of locations see Appendix 1)

Location of sample (ordered south to north)	% organic matter
Australind wetlands	94, 75
Riverdale wetlands	80, 90
Lake Mealup	96
Wawa Swamp	75
Forrestdale Road Swamp	78, 88, 77
Leda Swamp	95
Karrinyup Road Swamp	90, 75, 90
Lake Gwelup	78, 83, 84, 83, 89, 95,
Lake Goolelal	90
Beenyup Swamp central	78, 79
Beenyup Swamp south	79, 80, 81, 80, 81, 80, 95
Waluburnup Swamp	89
Ellenbrook Swamp	89, 83
Melaleuca Park	90, 75

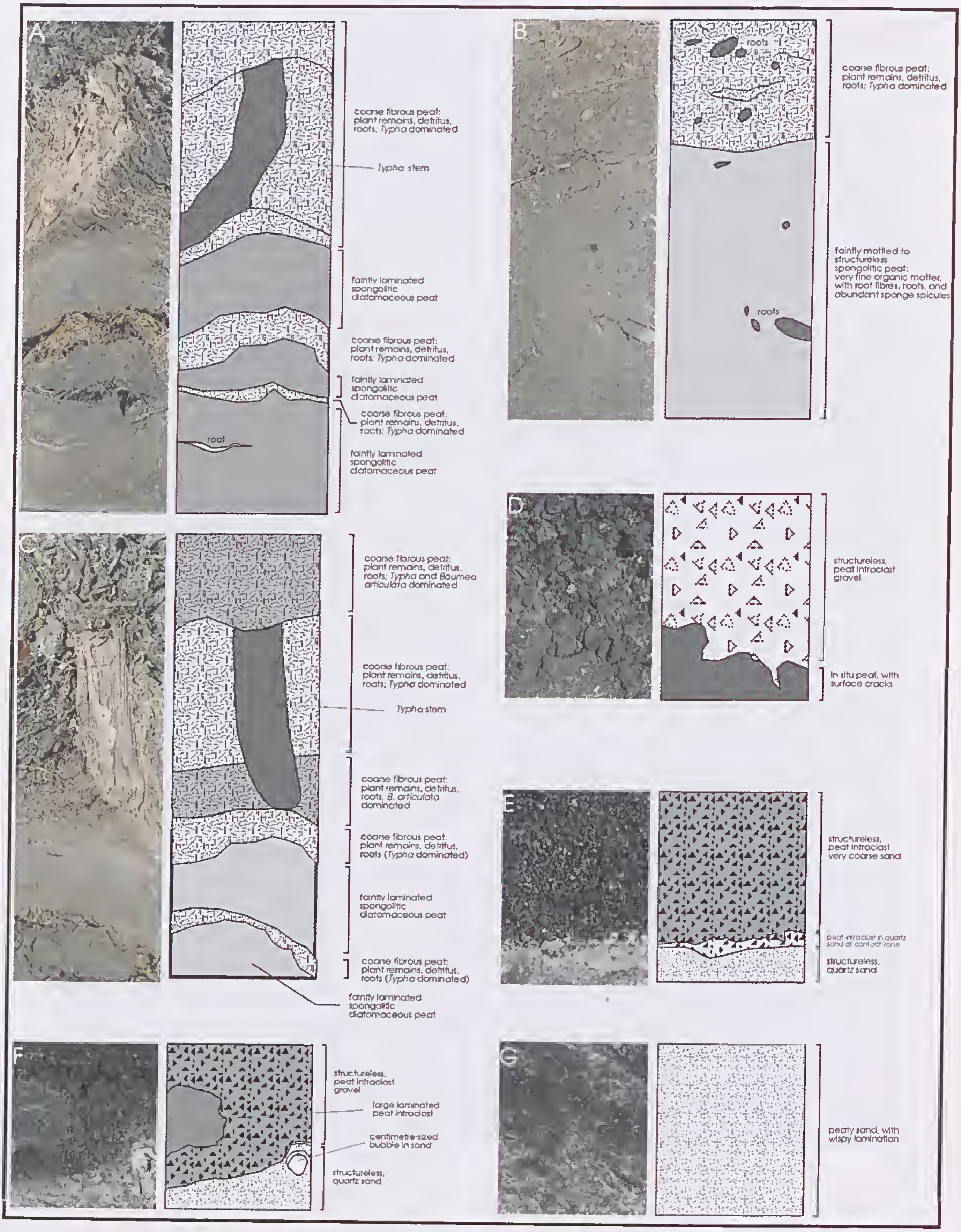
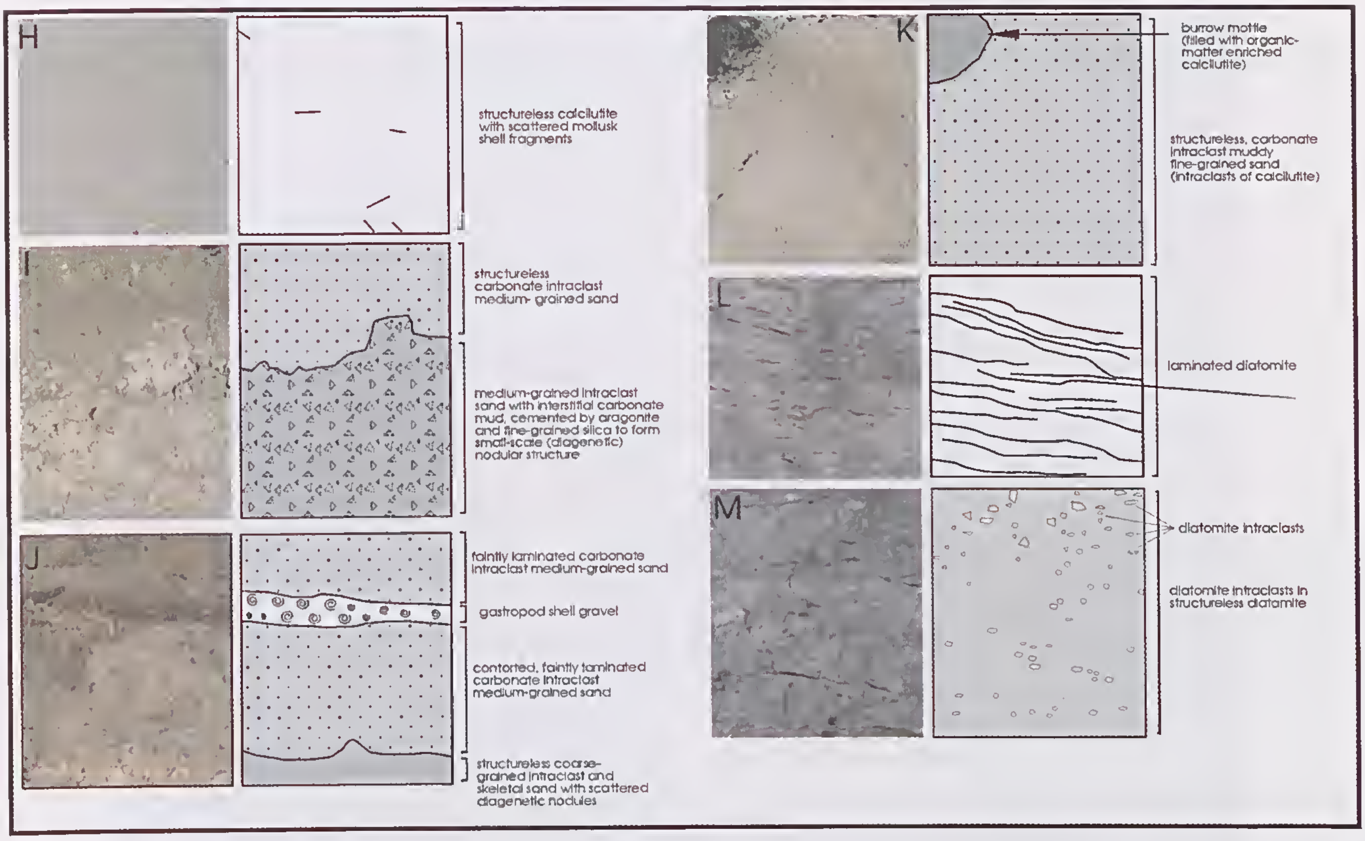

A
coarse fibrous peat: plant remains, detritus, roots; *Typha* dominated
Typha stem
faintly laminated spongolitic diatomaceous peat
coarse fibrous peat: plant remains, detritus, roots; *Typha* dominated
faintly laminated spongolitic diatomaceous peat
coarse fibrous peat: plant remains, detritus, roots; *Typha* dominated
root
faintly laminated spongolitic diatomaceous peat
B
roots
coarse fibrous peat: plant remains, detritus, roots; *Typha* dominated
faintly mottled to structureless spongolitic peat: very fine organic matter, with root fibres, roots, and abundant sponge spicules
roots
C
coarse fibrous peat: plant remains, detritus, roots; *Typha* and *Baumea articulata* dominated
coarse fibrous peat: plant remains, detritus, roots; *Typha* dominated
Typha stem
coarse fibrous peat: plant remains, detritus, roots, *B. articulata* dominated
coarse fibrous peat, plant remains, detritus, roots (*Typha* dominated)
faintly laminated spongolitic diatomaceous peat
coarse fibrous peat: plant remains, detritus, roots (*Typha* dominated)
faintly laminated spongolitic diatomaceous peat
D
structureless, peat intraclast gravel
in situ peat, with surface cracks
E
structureless, peat intraclast very coarse sand
peat intraclast in quartz sand at contact zone
structureless, quartz sand
F
structureless, peat intraclast gravel
large laminated peat intraclast
centimetre-sized bubble in sand
structureless, quartz sand
G
peaty sand, with wispy lamination

Figure 5. Annotated cores of selected sediments (width of all cores is 10 cm). A–C. Cores of peat. D–G. Cores of peat intraclast gravel and sand, quartz sand, and peaty sand. G–K. Cores of calcilutite, and carbonate intraclast gravel and sand. L–M. Cores of diatomite, and diatomite intraclast gravel.


H
structureless calcilutite with scattered mollusk shell fragments
I
structureless carbonate intraclast medium- grained sand
medium-grained intraclast sand with interstitial carbonate mud, cemented by aragonite and fine-grained silica to form small-scale (diagenetic) nodular structure
J
faintly laminated carbonate intraclast medium-grained sand
gastropod shell gravel
contorted, faintly laminated carbonate intraclast medium-grained sand
structureless coarse-grained intraclast and skeletal sand with scattered diagenetic nodules
K
burrow mottle (filled with organic-matter enriched calcilutite)
structureless, carbonate intraclast muddy fine-grained sand (intraclasts of calcilutite)
L
laminated diatomite
M
diatomite intraclasts
diatomite intraclasts in structureless diatomite

with fragments *c.* 1 cm (gravel-sized angular fragments of peat), down to sand size (Fig. 5D–F). Chemically, and in terms of the texture of the fine-grained organic matter that comprise the breccia clasts and sand, they are similar to the peat deposits described above. Structurally and granulometrically, however, the sediments are homogeneous, brecciated to conglomeratic, grading to sand-sized clasts of peat, or are layered with alternating grain size (pebble-sized, very coarse sand-sized, to coarse sand-sized fragments of indurated peat) of breccia and conglomerate, and locally root-structured. Texturally, these deposits consist of gravel to sand-sized angular to rounded clasts of peat set in a fine-grained organic matter < 63 µm in size, with root fibres, plant detritus particles and scattered quartz sand. Cores through peat intraclast gravel and sand show alternating grainsize-differentiated layers of peat clasts, and locally, vesicular structure.

Calcilutite

Calcilutite is cream, pink, or grey fine-grained carbonate sediment (Fig. 5H). The sediment is homogeneous, laminated, burrow-mottled, root-structured, bioturbated, or colour mottled. Texturally, the calcilutite consists of mixtures of silt-sized and clay-sized carbonate particles 63 µm to < 1 µm in size, ranging down to sediments composed dominantly of carbonate clay-sized particles, generally < 4 µm. Compositionally it is mainly calcite, with lesser amounts of organic carbon. In some wetlands, there is admixed Mg-calcite, aragonite and dolomite, and in some the muds are dominantly aragonitic. The sediment may contain freshwater snails and/or pelecypods, and ostracods, as gravel or sand-sized components, or their comminuted fragments, in layers, or scattered in random orientation throughout the sediment in low abundance (< 5%). The gradation of gravel and sand-sized particles through to clay-sized particles with consistent microstructure and ultrastructure throughout, together with the elemental composition determined by EDS, indicate that the < 63 µm fraction of carbonate particles is the accumulation of disintegrated (highly comminuted) mud-sized remains of charophytes and calcareous fauna such as molluscs and crustaceans. Reflecting the various biotic sources, calcilutite particle mineralogy may be calcite, low Mg calcite (Mg content 1–4%), high Mg calcite (Mg content 4–10%), and aragonite, with the particles deriving from calcitic shell, or disintegrated charophytes of calcitic or Mg-calcite mineralogy, or Mg-calcite shell, or aragonitic mollusc shell, respectively). The mineralogy of the mud also depends on the range of diagenetic precipitates that may occur within the sediment (*e.g.*, aragonite crystal sprays, or dolomite).

Using a modern species of *Chara* as an example, Figure 9 A,B,C illustrates the progression from 10–50 micron-sized aggregates (internally composed of units of micron-sized carbonate crystals), embedded in the walls of *Chara*, through to particulate carbonate sediment of micron-sized crystals. Calcilutite composed of fine-grained particles derived from invertebrate skeletons is shown in Figures 9 E & F. Similar transitions can be documented for the disintegration of carbonate-impregnated filamentous algae to calcitic and Mg-calcitic mud.

Carbonate skeletal gravel and sand

Carbonate skeletal gravel and sand are a cream or grey medium to coarse grained suite of sediments.

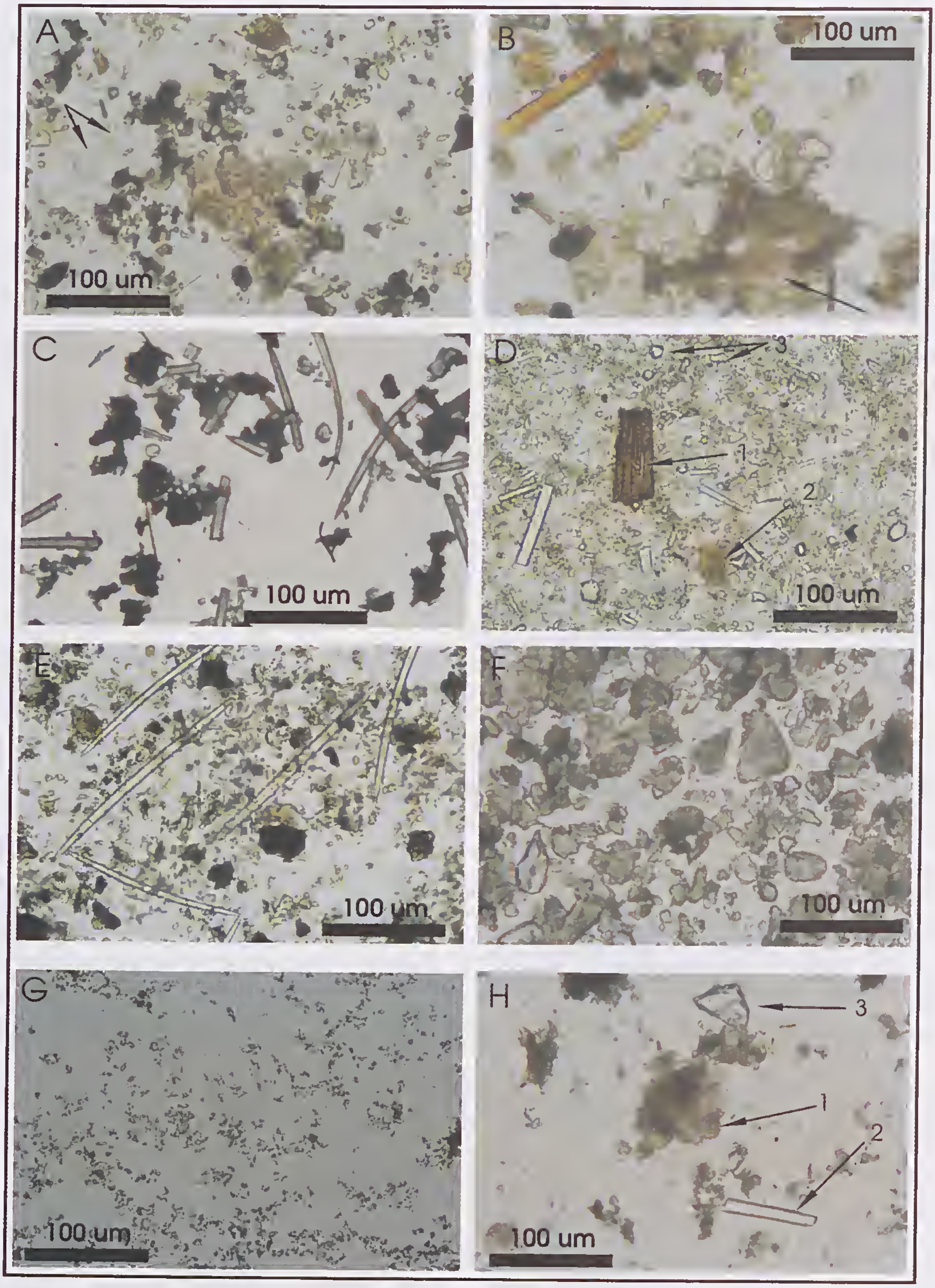


Figure 6. Annotated photomicrographs of standard particles in the fine-grained fraction of wetland sediments. Scale bar on all photomicrographs is 100 µm. Photomicrographs of the sand fraction is with reflected light through a stereoscopic microscope using a black background to the slide. All photomicrographs of the fine-grained fractions are using plane polarised transmitted light, except for (G), in which the light is partly cross-polarised. A. Organic matter (honey brown) in peat from Karrinyup Road Swamp, with scattered diatom debris (arrowed). B. Organic matter (brown and light honey brown) in peat from Karrinyup Road Swamp, with vestiges of cellular structure (arrowed) in the plant matter. C. Organic matter (dark particles) and sponge spicules and their fragments in peat from the shore of Lake Joondalup. D. Cellular plant material (arrow 1), homogenous plant material (arrow 2), quartz silt (arrow 3), and fragments of sponge spicules in a matrix of diatom silt; sample is the interstitial material from a diatomaceous peaty quartz sand. E. Sponge spicules in a diatom silt; sample of diatomite from wetland basin within Bassendean Dunes area east of Yanchep. F. Interstitial material from a kaolinitic muddy sand; the dominant mineral is kaolinite, with scattered quartz silt. G. Fine-grained calcite particles from a calcilutite, Lake Coogee. H. Carbonate intraclast (arrow 1), broken sponge spicule (arrow 2), and quartz silt (arrow 3) from a carbonate intraclastic sediment from Lake Coogee.

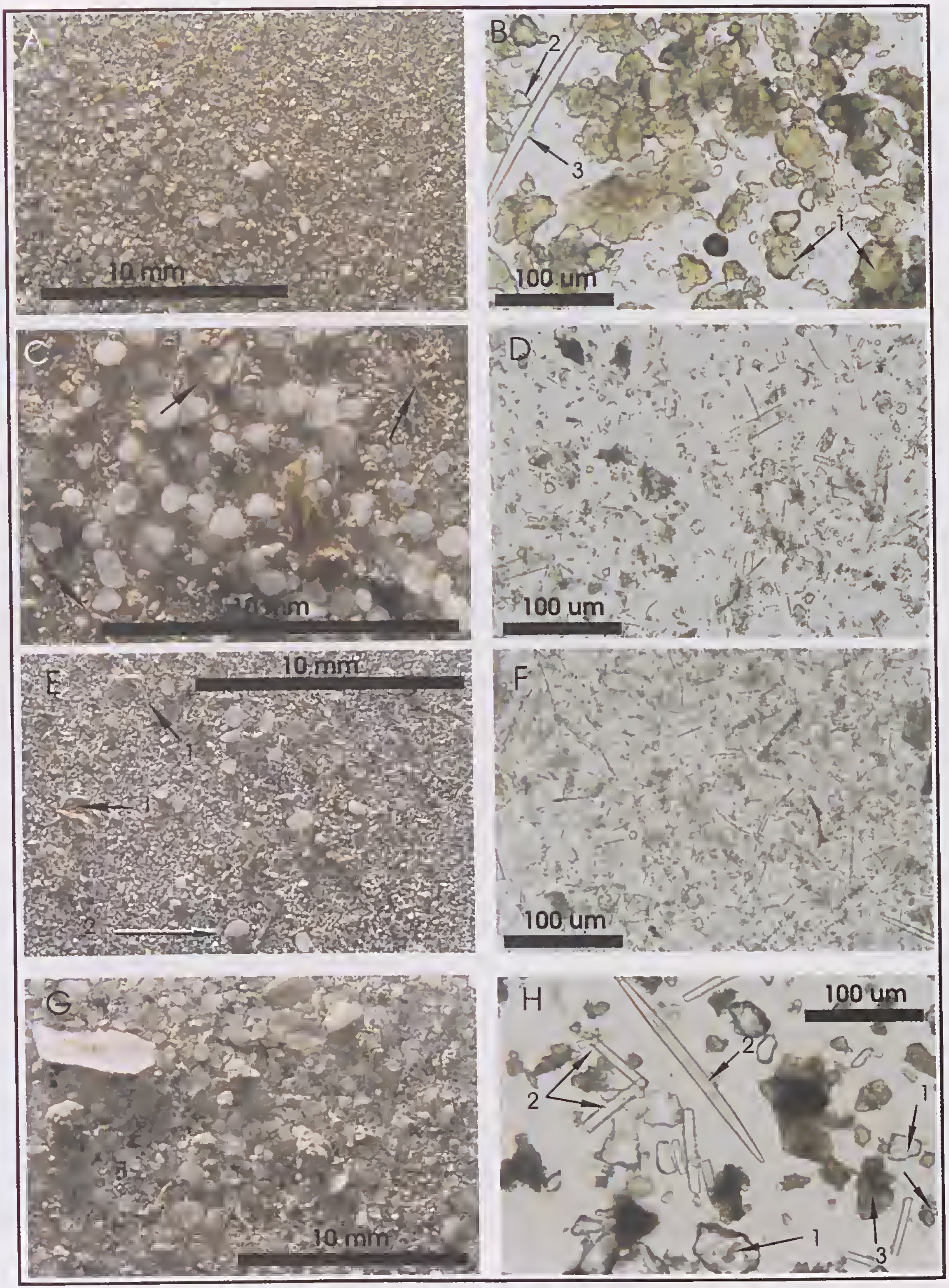


Figure 7. Paired annotated photomicrographs of grain mounts and mud particle mounts of the gravel-sized, sand-sized, and the fine-grained fractions of wetland sediments to illustrate their characteristics. For correlation of these photomicrographs with the description of the wetland setting and the wetland sediments, see Appendices 2 & 3. Scale bar on all photomicrographs of the sand fraction is 10 mm. Scale bar on all photomicrographs of fine-grained sediment is 100 μm. A & B: Sample No. 15 from Lake Mungala. A. Sand fraction of wetland sediment showing bleached and orange quartz sand grains. B. Mud-sized phyllosilicate minerals (arrow 1), quartz silt (arrow 2), and sponge spicule (arrow 3) comprising the fine-grained fraction of the sediment. C & D: Sample No. 18 from Melaleuca Park. C. Sand fraction of wetland sediment showing bleached quartz sand grains, and vegetation (root) fibres (arrowed). D. Hash of diatom frustule fragments and plant matter (dark grains) comprising the fine-grained fraction of the sediment. E & F: Sample No. 20 from Casuarina Swamp. E. Sand fraction of wetland sediment showing bleached quartz sand grains, fine sand-sized diatomite intraclasts, vegetation (root) fibres (arrow 1), and a rounded intraclast of diatomite (arrow 2). F. Hash of diatom frustule fragments comprising the fine-grained fraction of the sediment. G & H: Sample No. 32 from Bollard Bullrush Swamp. G. Sand and gravel fraction of wetland sediment showing bleached quartz sand grains, and mollusc gravel-sized and sand-sized skeletons. H. Quartz silt (arrow 1), sponge spicule and spicule fragments (arrow 2), and mud-sized phyllosilicate minerals (arrow 3) comprising the fine-grained fraction of the sediment.

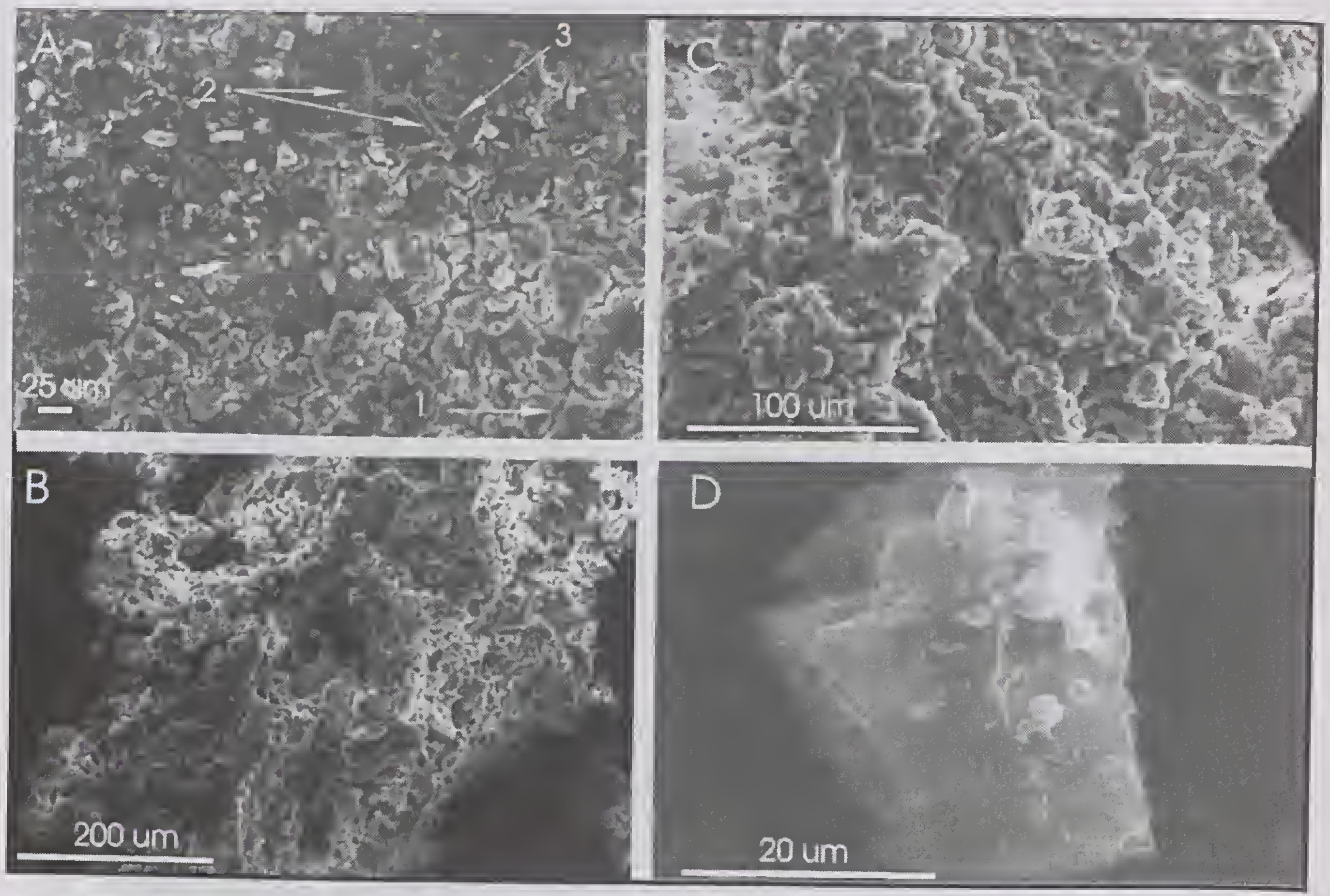


Figure 8. SEM photomicrographs showing features of peat. A. Overview of sample from Willie Pool showing general fine-grained nature of the peat (arrow 1; desiccation in the SEM photograph is due to the vacuum process), phytoliths (arrow 2), and root fibres (arrow 3). B. Plant detritus comprising the peat at Leda Swamp, showing material riddled with fungal hyphae and cavities produced by bacterial activity. C. Relict structures of plant detritus, here riddled with fungal hyphae and cavities produced by bacterial activity. D. Close-up of plant detritus from peat at Leda Swamp.

Structurally, the sediments are homogeneous to layered. Where sand-sized, the sediments grade from very coarse to medium sand. Compositionally, the sediments consist of whole and fragmented skeletons of molluscs, gastropods and/or pelecypods, and locally ostracods. The sediments commonly form layers in carbonate mud or peat deposits (Fig. 5J).

Carbonate intraclast gravel and sand

Carbonate intraclast gravel and sand are a cream or grey medium grained to coarse grained suite of sediments. They have homogeneous to layered structure, and local vesicular to fenestral structures (Fig. 5I–K). Texturally, where sand-sized, the grade is medium, coarse to very coarse grained. Compositionally, four types of intraclast are recognised: 1. clasts of calcilutite that essentially were dried, fragmented and reworked into intraclast sand; 2. clasts of carbonate cemented calcilutite, reworked into intraclast gravel and sand; 3. clasts of carbonate cemented intraclast sand (polycyclic intraclasts), reworked into intraclast gravel and sand; and 4. clasts of carbonate cemented skeletal sand, reworked into intraclast gravel and sand. Carbonate intraclast gravel and sand has formed within wetland basins, and particularly along their margins, where desiccation has cracked and fragmented calcilutite deposits, and high water wave conditions have reworked and rounded them to form thin shoreline deposits (Fig. 4A).

Diatomite

Diatomite is light grey fine-grained sediment, though locally dark grey to brown in organic-rich layers. It is homogeneous to root-structured at the surface, and laminated to structureless at depth (Fig. 5L). Grey to dark grey to brown diatomite has disseminated organic matter and/or fine-grained pyrite. Diatomite consists of silt-sized to clay-sized diatom skeletons and particles (Fig. 10). It may have scattered (< 5%) quartz sand and quartz silt. Diatomite ranges from porous sediment with low bulk density (composed of whole and fragmented diatom tests) to a compacted, dense sediment with relatively higher density (composed largely of wholly fragmented tests). This latter sediment, as mentioned earlier, has the bulk properties of a quartz siltstone or silt deposit (*i.e.*, not porous, but compact, and with a moderate bulk density unlike traditional "diatomaceous earth").

Diatomite intraclast gravel and sand

Diatomite intraclast gravel and sand are a light grey medium to coarse-grained suite of sediments, composed of rounded fine gravel to sand-sized sized clasts of diatomite (Fig. 5M). Diatomite intraclast gravel and sand form within wetland basins, and particularly along their margins, where desiccation has cracked and fragmented diatomite deposits and high water wave conditions have reworked and rounded them to form thin shoreline

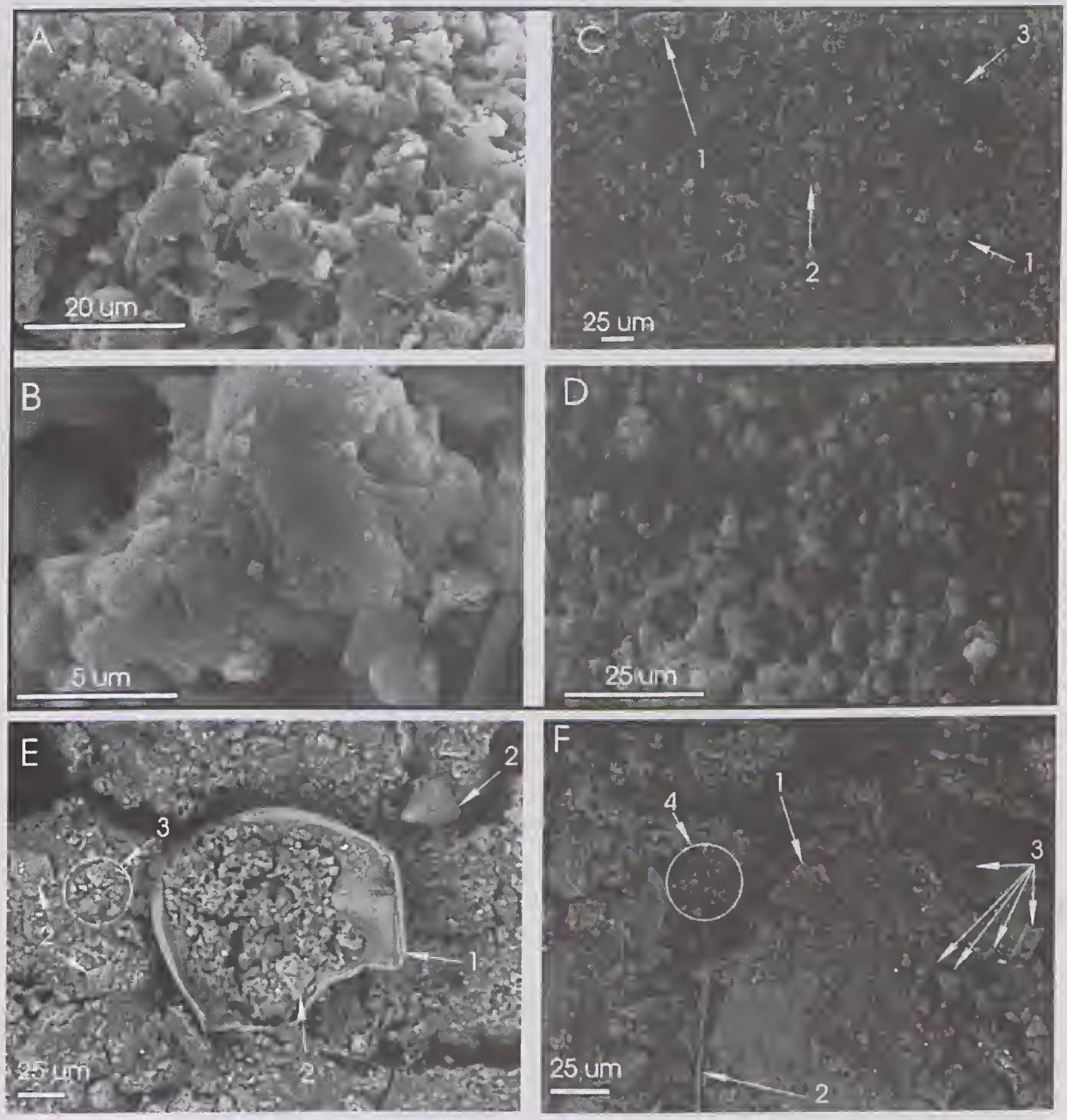


Figure 9. SEM photomicrographs showing nature of calcite impregnation of living *Chara*, and fine-grained constituents of calcilutite A. Overview of *Chara* exterior showing calcite crystals forming aggregates or clusters 10–20 µm in size. B. Close-up showing calcite aggregates in *Chara* with crystal components within aggregate from 5 to < 1 µm in size. Disintegration of these calcite aggregates will result in polycrystalline particles c 5 µm in size down to single unit crystal particles c 1 µm in size. C. Calcilutite from Lake Coogee showing various aggregates and sizes of carbonate grains, and their progressive disintegration from larger fragments of *Chara*, 25–30 µm in size (arrow 1), to smaller crystals, 1–4 µm in size (arrow 2); invertebrate skeletal fragments are scattered in the sediment (arrow 3). D. Close-up of calcilutite from Lake Forrestdale showing general fine-grained nature of the carbonate crystals 1–2 µm in size to < 1 µm in size, similar to crystal size and morphology of calcite crystals shown in *Chara* in (B) above. E. Close-up of calcilutite showing progressive comminution of calcareous invertebrate skeletons to form silt and clay sized carbonate particles: sand-sized skeletal particle (arrow 1); skeletal fragments *c* 25 µm in size (arrows 2); circled area (arrow 3) where there is a range of skeletal particle sizes from 10 µm to 1 µm in size. F. Close-up of calcilutite showing progressive comminution of calcareous invertebrate skeletons to form silt and clay sized carbonate particles: sand-sized skeletal particle (arrow 1) with perforated wall structure; coarse silt-sized skeletal fragment c 50 µm in size (arrow 2); a range of skeletal particles decreasing in size from 5–10 µm to 1 µm in size (arrows 3); circled area (arrow 4) where there is a range of skeletal particle sizes from 5 µm to 1 µm in size.

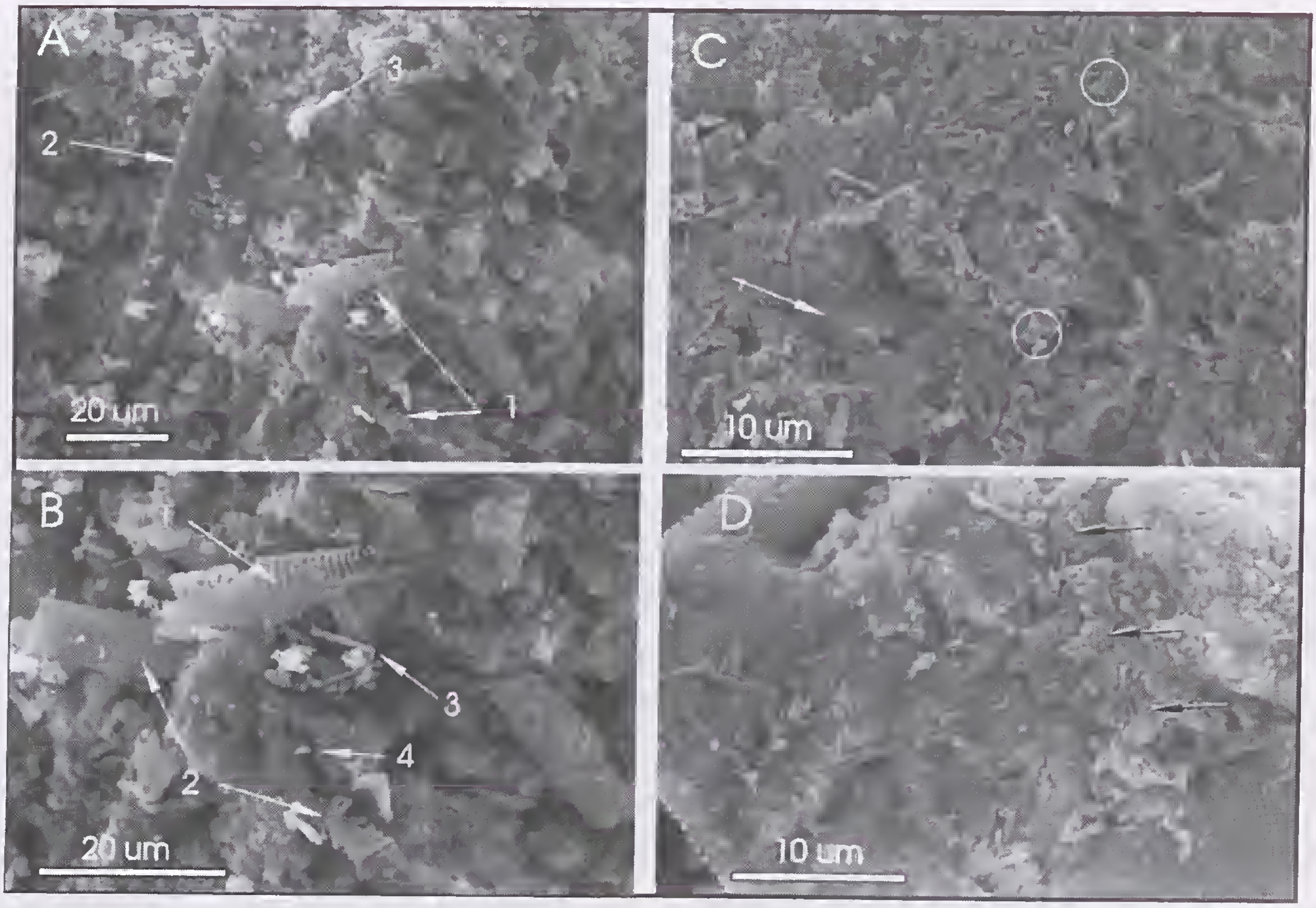


Figure 10. SEM photomicrographs of diatomite. A. Diatomite from a wetland basin in the Bassendean Dunes, east of Yanchep, showing typical view of diatom frustules in various stages of fragmentation (arrow 1), sponge spicule (arrow 2), and scattered kaolinite particles (arrow 3). B. Close-up showing the stages of fragmentation of diatom frustules: semi-complete diatom valve (arrow 1), 30 µm in size, fragmented valves (arrow 2) and (arrow 3), 15 µm in size, and 3–5 µm in size, respectively, leading finally to small fragments (arrow 4), < 1 µm in size. C. Close-up of diatomite from Lake Gnangara, showing diatoms in generally fragmented state; fragments show clear wall features such as sieve structure; particle sizes are mainly 1–5 µm; examples of diatom fragments < 1 µm in size are circled; the sample contains scattered quartz silt (arrow). D. Close-up of diatomite from Lake Gnangara showing diatom frustules in various stages of fragmentation from 3 µm in size, and showing wall structure (arrows), to 1–2 µm in size, and showing remnants of wall structure, to < 1 µm in size and structureless; the particles in this SEM view are adhering to a quartz silt particle (partial margin outlined).

deposits (Fig. 4B–G). Commonly, the intraclasts are embedded in a fine-grained diatomite matrix.

Kaolinitic mud

Kaolinitic mud deposits vary from white, orange, dark brown, and dark grey to black, and are homogeneous to root-structured. Locally, the mud beds exhibit polygonal cracks. Texturally, the mud deposits are composed of mostly clay-sized and silt-sized particles with scattered (< 5%) quartz sand. In sumpland and former sumpland basins, there also is occurrence within the kaolinitic mud of fragmented diatoms, sponge spicules and phytoliths. Compositionally, while these deposits are mainly kaolinite, locally, there may be some montmorillonite and fine-grained white micas such as muscovite or paragonite. Admixed with kaolinitic mud deposits also are small amounts of quartz and feldspar silt.

Quartz sand

Quartz sand is white, or light to dark grey deposit that is structurally homogeneous, bioturbated or root-structured, locally wispy laminated, and locally vesicular (Fig. 5E–F). In some areas, where freshwater crustacea are common, the sand is burrow-structured, with vertical burrows, up to several centimetres in diameter. Texturally, quartz sand is mostly well sorted, medium-grained and well rounded, though it may vary to poorly-sorted, mixed coarse, medium and fine in grainsize. Its composition is dominantly quartz, with minor feldspar, and minor amounts of heavy minerals.

Quartz silt

Quartz silt is cream to light grey, and structurally homogeneous to root-structured. It consists of silt-sized and some clay-sized silica particles, with scattered (< 5%) quartz sand. In sumpland and former sumpland basins, there is occurrence of fragmented diatoms, sponge spicules and phytoliths in the sediment. Deposits of quartz silt form only thin units in isolated wetlands.

Mixtures of sediments

While the sediments described above occur as end-member types, many wetland deposits are mixtures of these. The most important gradational series are between

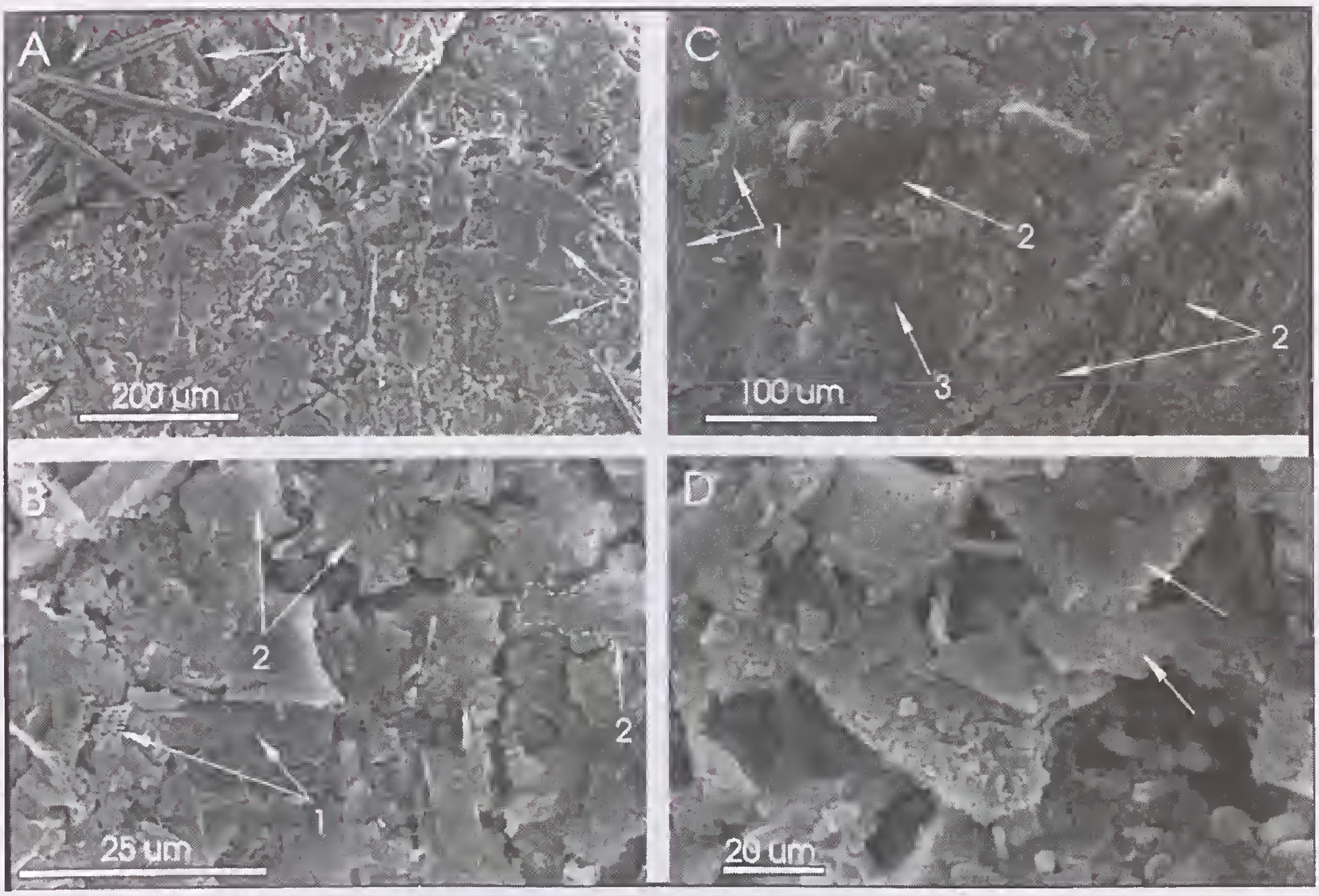


Figure 11. SEM photomicrographs of diatomaceous peat. A. Overview showing abundance of whole and fragmented sponge spicules, 200–250 µm in size (arrow 1), scattered diatom fragments (arrow 2), and the fine-grained organic matter that dominates the sediment, here showing cracking by desiccation (arrow 3), as a result of carbon-coating under vacuum in the SEM process. B. Close-up of typical fragments of diatom frustules, 5–20 µm in size (arrow 1), in various stages of disaggregation, and fine-grained plant detritus with layered internal structure (arrow 2). C. Overview of interstitial sediment of peaty sand from a wetland basin in the Ellenbrook area showing diatom fragments (arrow 1), plant remains and fibres (arrow 2), and phytoliths (arrow 3). D. Close-up showing diatoms in various stages of fragmentation from 20 µm in size to < 1 µm in size, and plant detritus (arrows).

the biogenic mud-sized sediments (*i.e.*, peat, diatomite and calcilutite), and between quartz sand and mud-sized components.

In the sediments dominated by biogenic mud-sized components, there may be a gradational series of sediment types between peat, diatomite, and calcilutite, *i.e.*, organic matter, diatoms and carbonate mud are mixed together to form a variety of mud-dominated sediments. Sponge spicules generally are not abundant enough in the wetland sediments to form spongolites, and hence in this paper are not considered to be an end-member biogenic sediment type. In this study they were most abundant in a thin layer of peaty sediment at Lake Gwelup, contributing *c.* 50% of particles to the sediment; in this context, the sediment is a spongolitic peat. A simplified classification and nomenclature of the three end-member biogenic fine-grained sediment classes and the sediments produced as mixtures of organic matter, diatoms and carbonate mud is presented in Figure 12A. The sediment types formed in this manner are: diatomaceous peat, calcilutaceous peat, organic matter enriched diatomite, organic matter enriched calcilutite, organic matter enriched diatomaceous calcilutite, diatomaceous calcilutite, and calcilutaceous diatomite (rare). The classification presented in Figure 12A involves only mixtures of biogenic mud-sized components and not mixtures of mud-sized and sand-sized components. Analyses from some 100 fine-grained wetland sediments are superimposed on the ternary diagram in Figure 13A to illustrate the variability in composition of these types of wetland sediments.

Generally, kaolinitic mud does not form significant mixtures with the biogenic muds. However, if there is admixed organic matter, carbonate mud, diatoms and kaolinite mud, the following nomenclature is proposed. With > 75% kaolinite, the sediment is kaolinitic mud. With 50–75% kaolinite, and diatoms or organic matter comprising the remaining 25–50% of the sediment, the sediment is termed diatomaceous kaolinitic mud, organic-matter enriched kaolinitic mud, or organic-matter enriched diatomaceous kaolinitic mud. With 25–50% kaolinite mud, the term "kaolinitic" becomes an adjectival descriptor to be added to one of the various mud sediment terms illustrated in Figure 12A, *e.g.*, kaolinitic organic matter enriched diatomite, or kaolinitic diatomaceous peat. Where the mud component is not kaolinite, the term "phyllosilicic mud" replaces "kaolinitic mud".

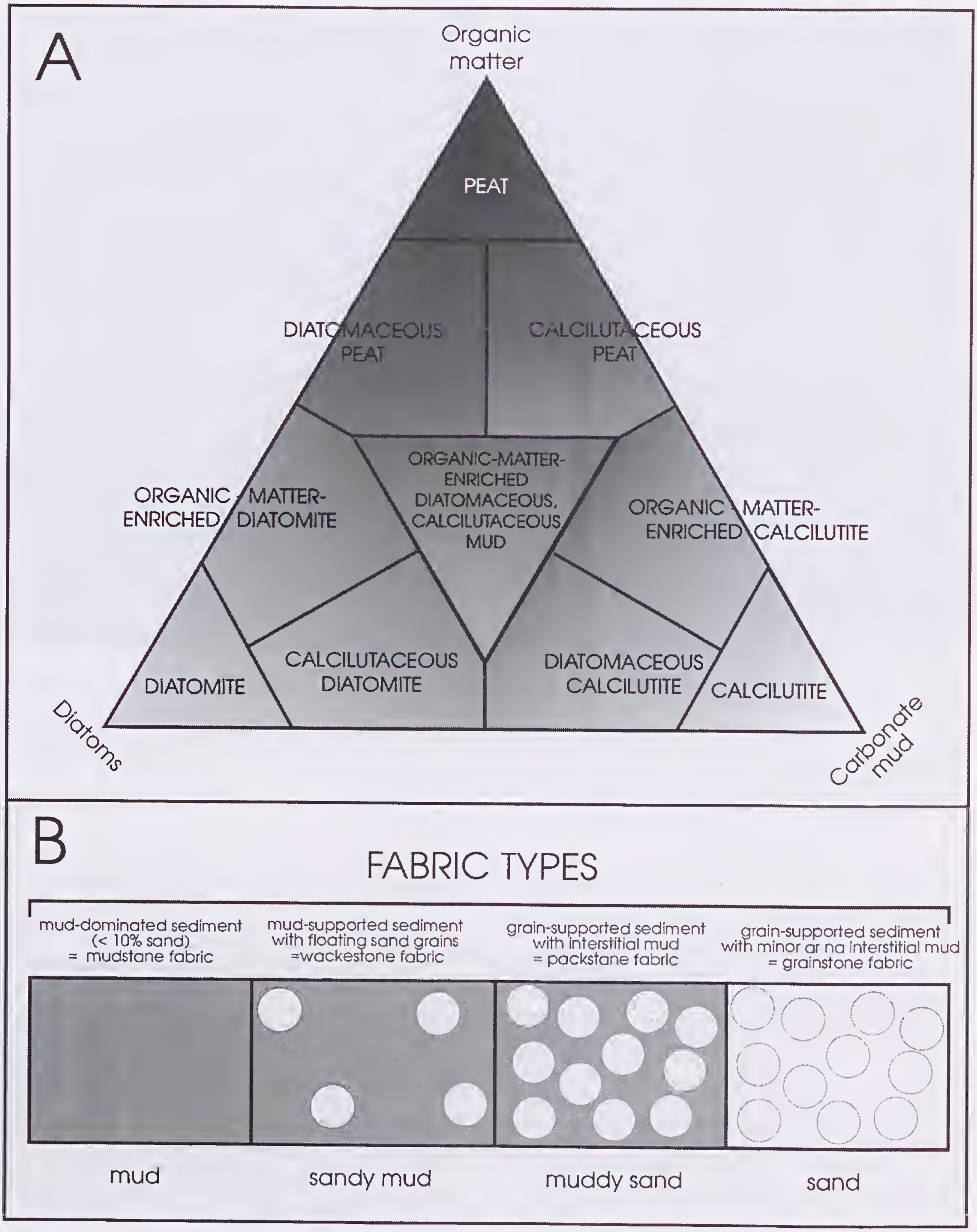

A
Organic matter
PEAT
DIATOMACEOUS PEAT
CALCILUTACEOUS PEAT
ORGANIC-MATTER-ENRICHED DIATOMACEOUS, CALCILUTACEOUS MUD
ORGANIC-MATTER-ENRICHED DIATOMITE
ORGANIC-MATTER-ENRICHED CALCILUTITE
DIATOMITE
CALCILUTACEOUS DIATOMITE
DIATOMACEOUS CALCILUTITE
CALCILUTITE
Diatoms
Carbonate mud
B
FABRIC TYPES
mud-dominated sediment (< 10% sand) = mudstone fabric
mud-supported sediment with floating sand grains =wackestone fabric
grain-supported sediment with interstitial mud = packstone fabric
grain-supported sediment with minor or no interstitial mud = grainstone fabric
mud
sandy mud
muddy sand
sand

Figure 12. A. Ternary diagram illustrating the categories and the proposed nomenclature for fine-grained sediment types that occur as end-members or as mixtures involving organic matter, diatoms, and carbonate mud. B. Conceptual diagram illustrating the intergradational sediment fabrics, from grain-support to mud-dominated (after Dunham 1962), used to partition the range of sediment types between sand and mud, with intermediates of muddy sand and sandy mud. The terminology of the mud fraction in the muddy sands and sandy muds follows the classification in (A) above. Also see text for explanation, and Appendix 3 for application of the classification.

Table 5

Categories of sediments transitional between sand and mud (fabric nomenclature after Dunham 1962)

Sediment fabric category	Wetland sediment type
composed wholly of sand grains in grain-support fabric (= grainstone fabric of Dunham 1962)	sand
composed of sand grains in grain-support fabric with interstitial mud (= packstone fabric of Dunham 1962); categorisation of interstitial mud follows Figure 12A	peaty sand, diatomaceous muddy sand, calcilutaceous muddy sand, kaolinitic muddy sand, organic matter enriched diatomaceous muddy sand, organic matter enriched calcilutaceous muddy sand,
composed of sand grains floating in a mud-support fabric (= wackestone fabric of Dunham 1962); categorisation of mud follows Figure 12A	sandy peat, sandy diatomite, sandy calcilutite, sandy kaolinitic mud, sandy organic matter enriched diatomite, sandy organic matter enriched calcilutite
composed wholly of mud-sized particles (= mudstone fabric of Dunham 1962); categorisation of mud follows Figure 12A	peat, diatomite, calcilutite, kaolinitic mud, organic matter enriched diatomite, organic matter enriched calcilutite

In regards to the gradation between quartz sand and mud-sized components (*i.e.*, quartz sand and peat, diatomite, calcilutite, or kaolinitic mud), the intermediates are peaty quartz sand (Fig. 5G) and sandy peat, diatomaceous (muddy) quartz sand and sandy diatomite, calcilutaceous (muddy) quartz sand and sandy calcilutite, and kaolinitic muddy sand and sandy kaolinitic mud, respectively (Table 5). There also are intermediates between intraclast sand and calcilutite (Fig 5K) and diatomite intraclast sand and diatomite. A simplified classification and nomenclature of the fabric classes and hence sediment classes for the mixtures between sand and mud is presented in Figure 12B. Fabric rather than percentage boundaries are used to separate the classes of muddy sand and sandy mud because the category of "grain-support" will have different size of interstitial space, and hence different sand to mud ratio, dependent on grain shape and sphericity (*e.g.*, Plates I & II of Dunham 1962). While the descriptor terms "peaty", "diatomaceous", and "calcilutaceous" carry implication that these sediment types are muddy sands, we suggest that the term "muddy" be inserted between the descriptors referring to the mud fraction and the term "sand", *e.g.*, calcilutaceous muddy sand. If the mud-sized fraction is left undifferentiated as to its particle types, the sediments may be termed "muddy sand" or "sandy mud". If the composition of the muddy component of the sediment is known and has been classsified as to its position on the ternary diagram, the category of the "mud" in the muddy sand can be adfixed to the sediment name. e.g., organicmatter enriched diatomaceous muddy sand. Analyses of the fine-grained interstitial material from some 50 wetland sediments are superimposed on the ternary diagram in Figure 13B to illustrate the variability in composition of the interstitial material in these types of wetland sediments.

The "muddy" sands are intermediate sediment types between wetland sands and biogenic muds and usually form where peat, diatomite, or calcilutite accumulations are interspersed with the influx of quartz sand from wetland basin margins (Fig. 4H), or at the basal transitional infiltrational zone where the fine-grained wetland sediment fill stratigraphically rests on the underlying basement sand (Fig. 14). In the cases of peaty quartz sand, diatomaceous quartz sand, and calcilutaceous quartz sand, the mud-sized components are interstitial to the grain-support sand framework. In the cases of sandy peat, sandy diatomite, sandy calcilutite, and sandy kaolinitic mud, quartz sand is dispersed in the mud-support matrix.

While phytoliths are not abundant enough in the sediments encountered in this study to constitute an end-member wetland sediment type, locally they comprise the dominant interstitial fine-grained component of muddy sands. In this context, these sediments are termed phytolithic muddy sand.

The range of common wetland sediments encountered in this study is listed in Table 6.

Table 6

Range of most common wetland sediments encountered in this study

peat
diatomite
calcilutite
kaolinitic mud
quartz sand
quartz silt
skeletal gravel and sand
peat intraclast gravel and sand
carbonate intraclast gravel and sand
diatomite intraclast gravel and sand
peaty quartz sand
sandy peat
diatomaceous muddy quartz sand
sandy diatomite
calcilutaceous muddy quartz sand
sandy calcilutite
kaolinitic muddy quartz sand
sandy kaolinitic mud
diatomaceous peat
organic matter enriched diatomite
sandy organic matter enriched diatomite
calcilutaceous peat
organic matter enriched calcilutite
sandy organic matter enriched calcilutite
organic matter enriched diatomaceous calcilutite
sandy organic matter enriched diatomaceous calcilutite
organic matter enriched kaolinitic mud
organic matter enriched diatomaceous kaolinitic mud
phytolithic muddy sand

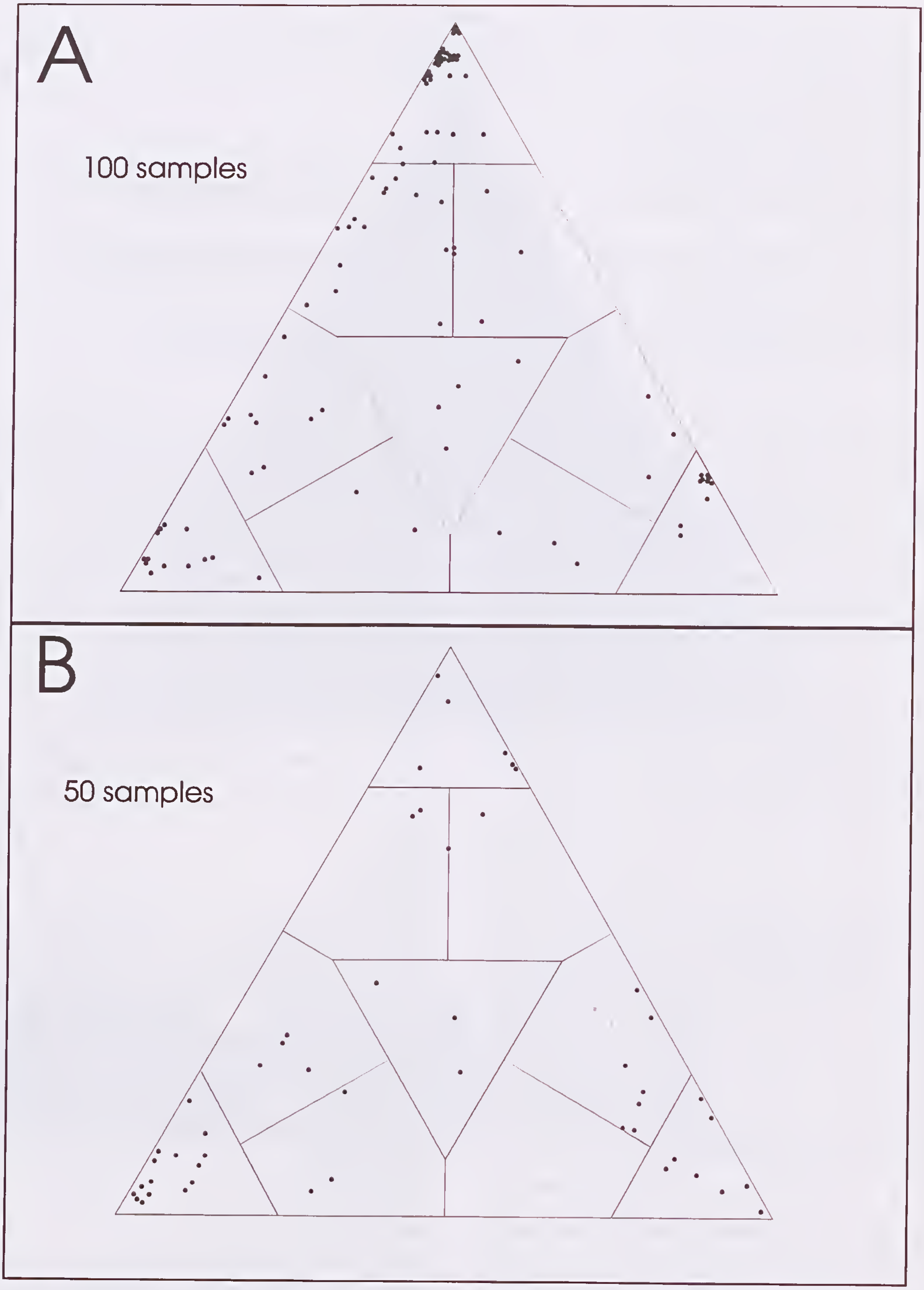


Figure 13. Ternary classification diagram of wetland sediment with superimposed results of laboratory analyses of a range of wetland sediments showing the variability of their composition. A. Results using 100 fine grained biogenic wetland sediments. B. Results using the fine grained material occurring interstitially in 50 wetland "muddy" sands.

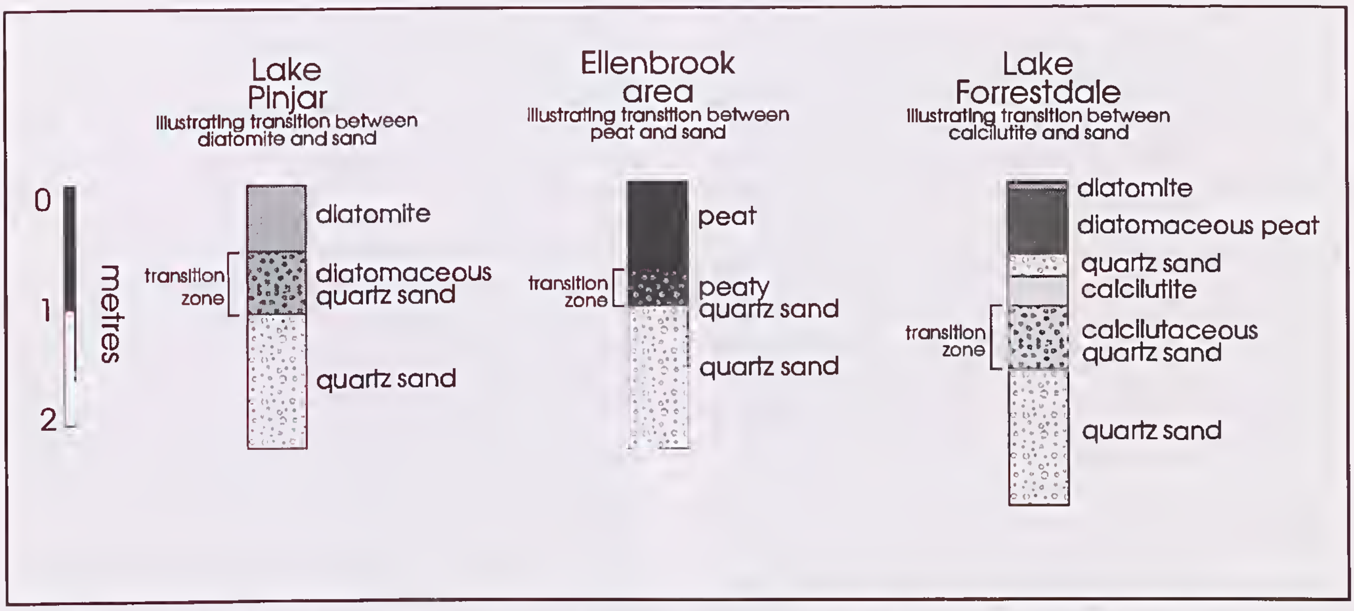


Figure 14. Examples of typical transitions of fine-grained wetland sediment (diatomite, peat, and calcilutite) into underlying basement sand to form "muddy" sand (specifically, diatomaceous sand, peaty sand, and calcilutaceous sand, respectively).

Suggested use of descriptors

The various sediment types described above can be discriminated further by use of adjectival descriptors, the most important of which are the subdominant to minor grain content, the sedimentary structures, colour or tone, and sand grain-size. For example, as noted earlier, sponge spicules do not form "spongolite" as an end-member sediment type, but they may comprise a conspicuous and/or subdominant proportion of peat and diatomite. In this context, their presence is noted by an adjectival descriptor, *viz*., spongolitic peat, or spongolitic diatomite. Similarly, if diatoms make a conspicuous contribution to the sediment, the descriptors "diatomaceous" are added to the primary sediment term, *e.g*., diatomaceous kaolinitic muddy sand. Using sedimentary structures, for instance, calcilutite can be separated into laminated calcilutite, massive calcilutite, mottled calcilutite, and peat can be separated into massive peat, fibrous peat, laminated peat. Sediments and soils may be characterised by their colour or tone (*e.g*., dark grey, cream, yellow), with the caveat that colour and tone may be a primary sediment attribute (*e.g*., the colour of accumulated charophytes), or may be the result of diagenesis (*e.g*., formation of fine-grained pyrite). Sand and gravel deposits may be divided into grades of grain-sizes (using terms of Wentworth 1922), *e.g*., medium carbonate intraclast sand, or coarse peat intraclast sand.

The protocol for ordering the descriptors where there are a range of particle types contributing to, say, the muddy fraction, the name of the most abundant particle type is placed closest to the core sediment term. Thus, a spongolitic phytolithic diatomaceous muddy sand is muddy sand with mud-sized particle abundance diatoms > phytoliths > sponge spicules.

Processes affecting and influencing sedimentation in wetlands

Large-scale and small-scale processes influence wetland sedimentation on the Swan Coastal Plain. They are instrumental in directly contributing sediment to wetland basins, in influencing and altering the structures of sediments, and effecting changes texturally and compositionally. The large-scale processes are sedimentary, geomorphic and hydrological, while the small-scale processes encompass the physical, biological and chemical.

At the large scale, the geomorphic/geologic setting has an influence on the type of physical and chemical processes that operate within the wetland. For example, the geomorphic/ geologic setting affects sedimentation through direct input of sediment, but also by determining the type and impact of sediment transporting agents that will be present, such as fluvial influx or aeolian contribution. The large-scale geomorphic/geologic setting also influences the hydrological and hydrochemical setting of a wetland, and this influences the development of various chemical environments for surface and ground waters. For instance, wetlands in a terrain of yellow quartz sand receive quartz sand into the basin through aeolian transport, whereas wetlands in terrains near Holocene coastal dunes may receive quartzo-calcareous sediment through a similar agent or through encroachment of dunes. Wetlands in quartz sand terrains will have a different groundwater chemistry to those in limestone terrains.

At the smaller scale, physical processes operating in and around wetlands that influence sedimentation and sedimentary products include: 1. sheet wash from the adjoining uplands to provide sediment fill into the wetland; 2. aeolian deposition and deflation (aeolian delivery of extrabasinal particles is evident as quartz silt and quartz very fine sand scattered in central basin deposits of peat, calcilutite, and diatomite); 3. wave action in standing water during high water periods to effect sediment winnowing, transport and the development of peripheral low-relief sandy beachridges or beaches, and the wave reworking of any sandy shores of wetlands that are bordered by sand terrain; 4. transport as a suspension load of fine-grained particles such as diatoms, organic matter, or carbonate mud from peripheral zones into deeper water, and its settling on the basin floor as ooze; 5 transport of fine-grained particles (such as diatoms) from a dried wetland floor towards the shore by aeolian processes to form low relief supra-littoral to littoral shoreline "mud" ridges; 6. the desiccation of any muddy margins of wetlands, and later in the dry season, the desiccation of the centre of wetlands if exposed; 7. local fluvial input (*i.e.*, from local channels along the wetland margin, and that are consequent to the wetland shore); 8. groundwater discharge (seepage and percolation) to deliver fine-grained sediment in suspension and to initiate chemical changes; 9. groundwater fluctuation to initiate chemical changes; and 10. evaporation resulting in soil desiccation, and in changes in water chemistry.

Examples of small-scale biological processes within wetlands include organic accumulation of detritus from flora and fauna (these include *in situ* peat beds, diatom deposits, and local shell beds), the contribution of calcitic mud by the disintegration of semi-calcareous charopyhtic algae, and bioturbation by flora and fauna (such as freshwater crustacea, insects, tortoises, reptiles, amphibians, and mammals), and the root-structuring and burrow-structuring of sediments by the biota. Bioturbation by fauna such as frogs, bandicoots, ants, and freshwater crustacea is particularly significant in the marginal facies of wetlands where interlayered sediments may be mixed, or the sediment becomes burrow-structured or burrow-mottled. Shoreline and peripheral vegetation also function in the role of sediment trapping, binding and root-structuring, and contributing directly to the sedimentary deposit as *in situ* deposits of plant material.

Examples of small-scale chemical processes within wetlands include (1) the initiation of chemical changes due to sediment influx via seepage and percolation, (2) the initiation of chemical changes due to sediment transfer via vertical water fluctuations, and (3) changes in water chemistry due to evapo-transpiration. Chemical processes within wetlands that affect sediments include precipitation of minerals such as syntaxial overgrowths on grains, precipitation of minerals as intergranular cements (*e.g.*, calcite), the stripping of clay and iron oxides from Pleistocene yellow sand grains under acidic conditions, precipitation of iron oxides, the precipitation of iron sulphides, and the transport of ions and nutrients throughout the sediment column.

At the small scale, physical and chemical processes can often trigger biological responses which can then further influence sedimentation. With wave action on a standing body of water, for instance, the physical and chemical properties of surface water within wetlands in different geomorphic settings with different types of sediments in the basins, can determine the suspended sediment content or uptake of soluble material (*viz.*, mud-sized phyllosilicate mineral content, carbonate mud content, and tannin content), which will affect turbidity and water quality, with concomitant influence on planktonic and benthic biota.

Fire is another influence on stratigraphy, structure, texture, and composition of wetland sediments (Semeniuk & Semeniuk 2005b). *Pyrosediments*, a term coined in this paper, are secondary sediments, such as residues, formed as a result of the combustion of sedimentary materials. In natural settings, periodic fires, usually ignited by lightning in summer, may destroy peat beds and reduce a complex sequence of peats and other sediments to a more simple peat-free sequence. In modern times, fire may be anthropogenic or natural. By agency of fire, sand lenses can be introduced into a dominantly peat sequence by reducing to ash those trees with sand-constructed termitaria interior to their trunks. Fire in wetlands also can alter sediments texturally (*e.g.*, it can fracture susceptible grains by intense heat to finer grain sizes, and can generate surficial breccia), and create specific types of pyrogenic surfaces and structures, such as fire-sculptured surfaces, baked surfaces, iron-oxide stained surfaces, and deep cracks, all of which influence development of subsequent sedimentary structures. Some of the buried surfaces and structures found in the subsurface in this study that had been generated as a result of fires are: buried fire-scarred (irregular to scalloped) surfaces; cracked surfaces (filled by later sediments, such as mud or intraclast breccia); *in situ* breccioid structures; and millimetre-scale lensoid structures resembling flaser layering (*cf.* Reineck & Singh 1980). Fire can also alter wetland sediment composition: pyrite is transformed to iron oxides, biogenic silica is partly transformed to crystalline silica, and wood is transformed to ash of calcite, halite, sylvite, and anhydrite (later altering to gypsum).

Diagenetic effects and overprints on wetland sediments and adjoining materials

There are chemical, biological and physical diagenetic effects on wetland sediments, but the main effects are chemical. The chemical effects and overprints of diagenesis in wetland sediments include: 1. dissolution of shells and other carbonate grains; 2. precipitation of carbonates as isolated crystals, crystal aggregates, grain rimming cements, and nodules; 3. burning of wood, other vegetation,. and peat to generate calcite and anhydrite (and gypsum), and other minerals; 4. dissolution of diatoms and phytoliths; 5. precipitation of silica; 6. precipitation of iron oxides to form ferricrete; 7. precipitation of metal and metalloid sulphides (*e.g.*, iron sulphides such as framboidal pyrite, or marcasite, or arsenopyrites) to impart a light grey to dark grey hue to sediments; and 8. reduction of iron oxide in envelopes around sand grains to form sulphides, imparting a light grey to dark grey hue to sediments and adjoining materials. Only carbonate dissolution, carbonate cementation/nodulation, silica solution and re-precipitation, and ferricrete cementation/ nodulation are described further here.

In many wetland sediments, under conditions of acidic groundwaters, molluscan shells and carbonate intraclasts commonly exhibit varying degrees of surface corrosion. With molluscs, particularly within peats, there is gradation from entire shells through to pitted shells to heavily corroded shell and vestiges. Corrosion of carbonate intraclasts results in the pitting and development of micro-relief on their surface. Within carbonate sediments there is also re-precipitation of carbonate to form thin crusts, nodules, interstitial cement, or displacive crystal aggregates: calcite and Mg-calcite locally cements carbonate; in some wetlands, aragonite has been precipitated within host carbonate sediments as an intergranular cement in intraclast and skeletal gravel and sand, or as a displacive radiating aggregate of acicular crystals within fine-grained carbonate sediment. Dolomite also locally has formed as a diagenetic mineral in a carbonate mud host sediment (similar to The Coorong; von der Borch 1976; Rosen *et al.*, 1989).

The burning of wood, other vegetation, and sulphide-mineral-bearing peat in wetlands generates a range of minerals, evident in the ash: fine grained calcite, formed where Ca released in burning wood combines with CO_2 also released during the combustion; anhydrite, where Ca released in burning wood combines with SO_2 released during the combustion (anhydrite later transforms under waterlogged conditions to gypsum); halite and sylvite (formed from the Na and K released in combustion), both of which dissolve in the ensuing wet season; crystalline silica formed from biogenic silica; and goethite and haematite formed by oxidation of pyrite (Semeniuk & Semeniuk 2005c). In this context, with the alteration of pre-existing materials to pyrogenic calcite, crystalline silica, goethite and haematite, pyrogenesis is a subclass of diagenesis.

SEM shows that the biogenic silica of diatoms, sponge spicules and phytoliths also exhibit surface corrosion, and may be progressively chemically removed. In sediments where there is such dissolution, silica is locally re-precipitated, forming micro-botryoidal crusts and coatings to particles, indurating the sediment. Dissolution of biogenic silica and its localised re-precipitation as cements and nodules may occur in diatomites, carbonate sediments, and quartz sands,

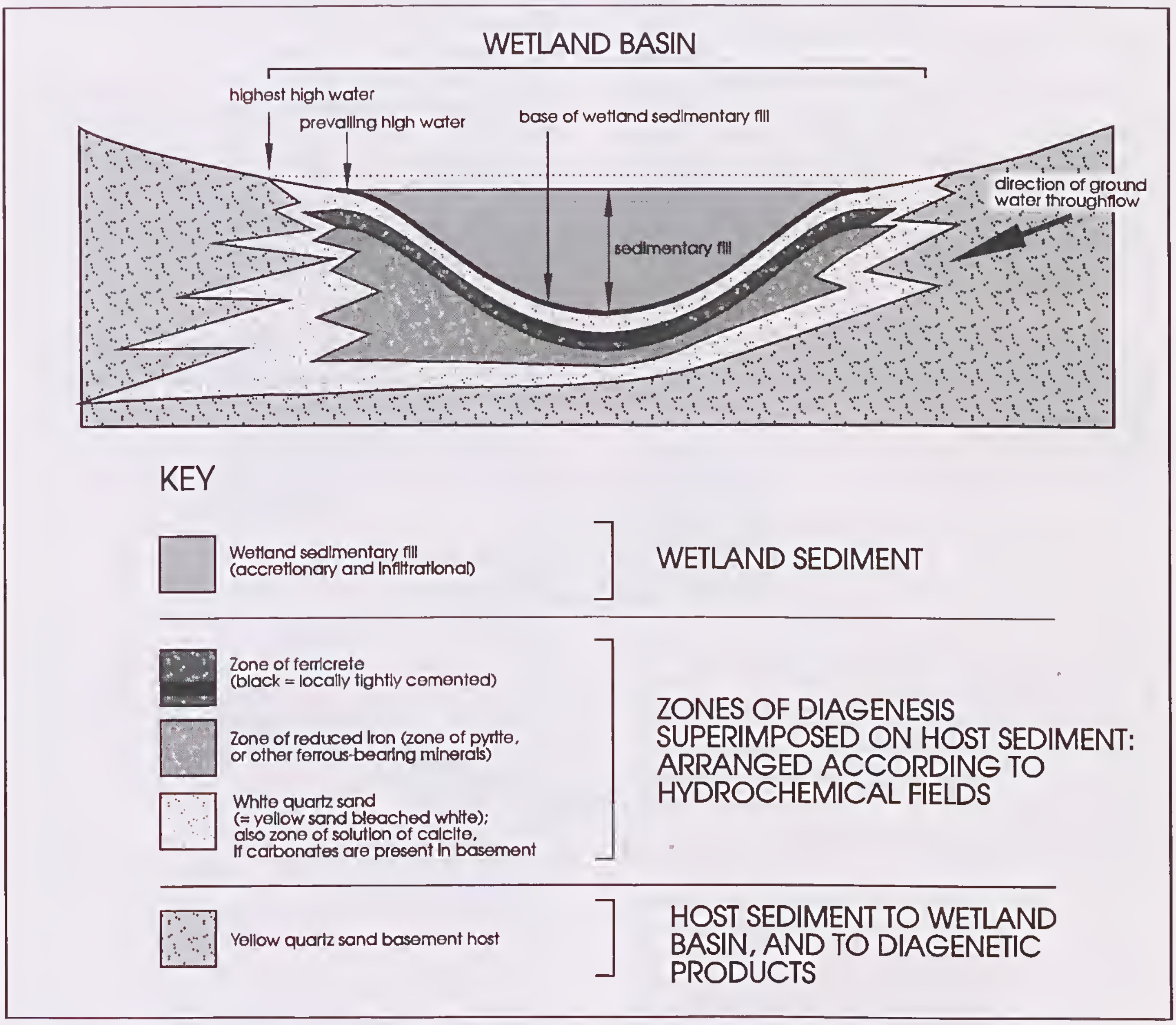

WETLAND BASIN
highest high water
prevailing high water
base of wetland sedimentary fill
sedimentary fill
direction of ground water throughflow
KEY
Wetland sedimentary fill (accretionary and infiltrational)
WETLAND SEDIMENT
Zone of ferricrete (black = locally tightly cemented)
Zone of reduced iron (zone of pyrite, or other ferrous-bearing minerals)
White quartz sand (= yellow sand bleached white); also zone of solution of calcite, if carbonates are present in basement
ZONES OF DIAGENESIS SUPERIMPOSED ON HOST SEDIMENT: ARRANGED ACCORDING TO HYDROCHEMICAL FIELDS
Yellow quartz sand basement host
HOST SEDIMENT TO WETLAND BASIN, AND TO DIAGENETIC PRODUCTS

Figure 15. Idealised diagram (not to scale) showing zones of diagenetic alteration under and around wetland basins resulting from the wetland hydrochemical fields interacting with the underlying and adjoining basement sand to illustrate that the products of diagenesis are separate from the sedimentary fill of a wetland basin. In this example, diagenetic zones focus on the chemistry of Fe, but similar zones may be devised for carbonate, silica, and phyllosilicate mineral components of the host sediments around and underlying wetlands. The asymmetry in the diagenetic zones is intended to show the effect of the directional plume of groundwater flow, with interdigitation reflecting lithological or hydrogeologic influences.

forming small nodules (of induration), or interstitial grain-coating fine-grained cement.

Ferricrete is common in wetlands as an indurated sheet overprinting sandy wetland fills at levels of the water table and below. The ferricrete is a mixture of goethite, X-ray amorphous iron oxides, infiltrated kaolinite, and silica silt. Where it occurs as a weakly indurated overprint, it forms laminated rims interstitial to sand grains. Well-indurated ferricrete consists of a complex of laminated iron oxides, kaolinite, and quartz silt filling the sand interstices.

There also are diagenetic effects on the materials underlying and adjoining the wetland sediments, but these strictly are processes and products associated with acidic and Fe-enriched water derived from wetlands on underlying basement materials (Fig. 15). It is useful to clearly separate the products of diagenesis on basement materials, and diagenetic effects on wetland sediments, from primary wetland sediments themselves. These diagenetic effects include the bleaching of yellow sand on the margins and beneath wetland basins, and the translocation of mud-sized phyllosilicate mineral particles and fine quartz silt down the profile or into a wetland. Thus, while wetland sediments may fill a basin, there also is a halo effect of diagenetic alteration from the base and margins of the wetland into the underlying materials. Pre-Holocene host sediment under wetland terrains, for instance, are commonly bleached to white sand, with incomplete bleaching resulting in mottled white, cream, yellow and orange coloured sand. The host sand is yellow to orange quartz sand where the sand grains are coated by goethite-impregnated kaolinite skins (as described above). The bleached sand is quartz sand stripped of the goethite, kaolinite and quartz silt. The mud-sized phyllosilicate mineral particles and fine quartz silt are translocated to elsewhere in the profile, and the goethite is chemically translocated to precipitate as an iron oxide to form ferricrete. This style of alteration around wetlands was described in Figure 10 of Glassford & Semeniuk (1990) for yellow sand proximal to and at the water table.

Origin of sedimentary particles and wetland sediments

The origin of wetland sediment particles and wetland sediment types is diverse, ranging from intrabasinal to extrabasinal, from terrigenous to biogenic sources, and for the intrabasinal, biogenic, and chemically modified sediments, from *in situ* accumulations to reworked deposits (Fig. 16).

The sedimentary particles and the accumulated deposits can be initially categorised as intrabasinal and extrabasinal, then further differentiated as infiltrational or accretionary. Wetland particles and sediments can also be differentiated as terrigenous (*i.e.*, derived from terrestrial sources, such as quartz sand and mud-sized phyllosilicate mineral particles), or biogenic (*i.e.*, derived from biological sources such as peat, carbonate sediment, and siliceous diatoms). In this context, peats, calcilutite,

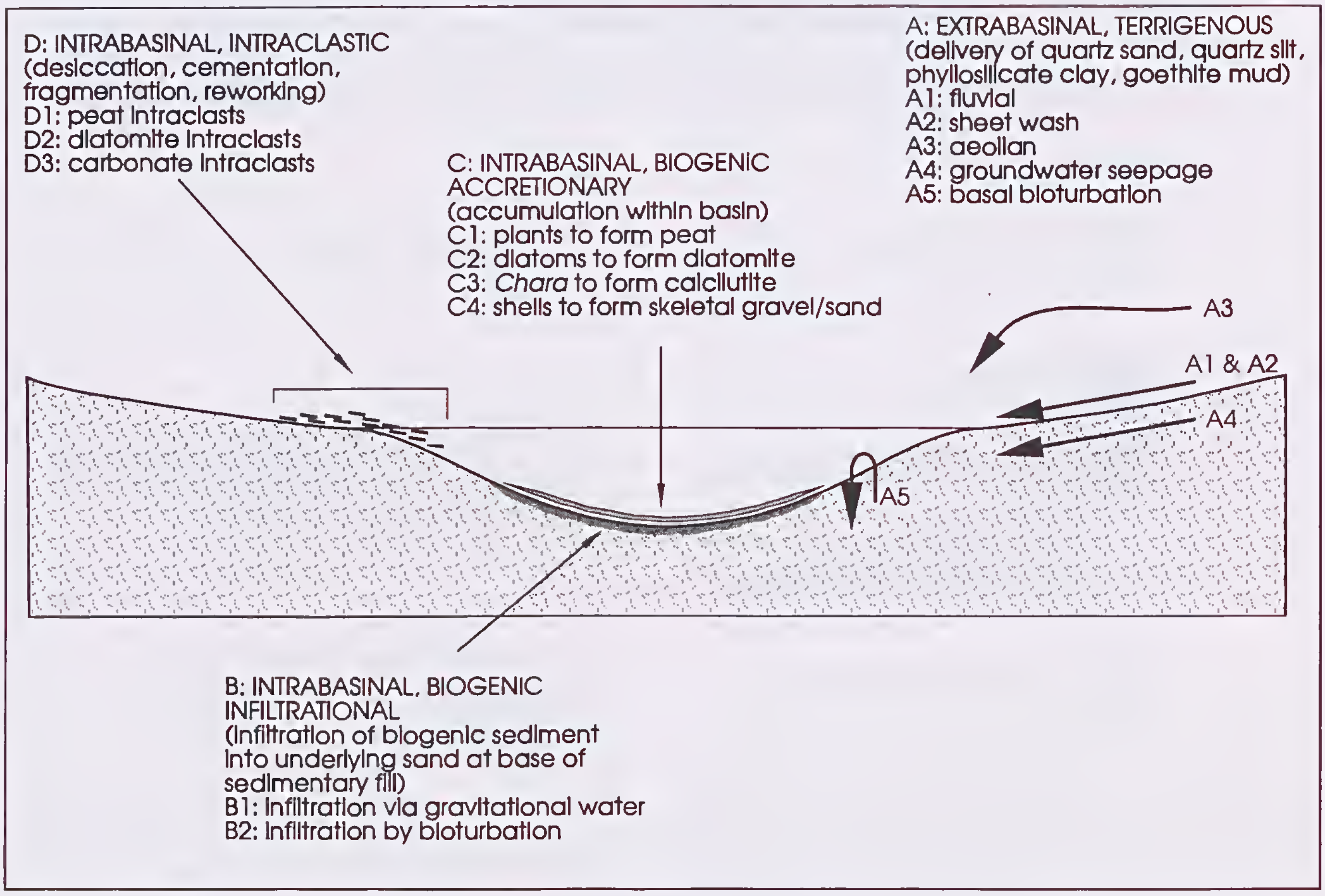

D: INTRABASINAL, INTRACLASTIC
(desiccation, cementation, fragmentation, reworking)
D1: peat intraclasts
D2: diatomite intraclasts
D3: carbonate intraclasts
C: INTRABASINAL, BIOGENIC ACCRETIONARY
(accumulation within basin)
C1: plants to form peat
C2: diatoms to form diatomite
C3: *Chara* to form calcilutite
C4: shells to form skeletal gravel/sand
A: EXTRABASINAL, TERRIGENOUS
(delivery of quartz sand, quartz silt, phyllosilicate clay, goethite mud)
A1: fluvial
A2: sheet wash
A3: aeolian
A4: groundwater seepage
A5: basal bioturbation
A3
A1 & A2
A4
A5
B: INTRABASINAL, BIOGENIC INFILTRATIONAL
(infiltration of biogenic sediment into underlying sand at base of sedimentary fill)
B1: infiltration via gravitational water
B2: infiltration by bioturbation

Figure 16. Origin, categories and composition of wetland sediments.

and diatomite are intrabasinal biogenic deposits in that they are definitively restricted to the wetland basin and have formed in response to water chemistry. They are also the most common accretionary deposits. Quartz sand and mud-sized phyllosilicate mineral particles are extrabasinal, since their source can be unequivocally demonstrated to be the wetland margins. The transitional muddy sediments (with the mud component being diatoms, calcilutite, or phyllosilicate mineral particles) at the base of wetland fills commonly are infiltrational, in that they have formed by the introduction of intrabasinal sediment into the underlying basement sand (Fig. 16). Muddy sediments also form along wetland margins, and here they can be accretionary in that the fine-grained component is intrabasinal, and it is mixed in with extrabasinsal sand derived by sheet wash from the surrounding uplands.

Particles and material are contributed to the sediments by the variety of biota that inhabit or visit wetlands. These particles and materials from extrabasinal sources include scats, skeletons, foreign plant material, and imported food remains from vertebrates such as reptiles and mammals, and invertebrates such as insects. Intrabasinal particles and materials include mollusc shell, other skeletons from vertebrates (*e.g.*, fish) and invertebrate fauna, tests, sponge spicules, crustacean exoskeletons, zooplankton tests, as well as plant remains from *in situ* trees and shrubs (trunks, branches, leaves, roots, flowers, fruit), herbs and sedges, algae, and phytoliths and diatoms. Biogenic silica (as diatoms, sponge spicules, and phytoliths) is conspicuous, ubiquitous, and important in wetland sediments. Diatom frustules, and fragments, for instance, can occur in a range of wetland sediment deposits, constituting a significant proportion of peaty sediments; similarly, sponge spicules contribute to peaty sediments, as well as to diatomites, and phytoliths also make contributions to wetland deposits as intrabasinal particles, especially in peats, though overall they remain in relatively low concentrations in the sediments.

Peat in wetlands derives from vegetation detritus. Under acidic and anaerobic conditions within the substrate, and under water, aerobic bacterial decay of vegetation detritus is arrested or reduced, and plant detritus cumulatively accretes to form organic-rich beds, with anaerobic microbial and fungal breakdown of the material. Sites of high vegetation productivity, coupled with low rates of organic decay, combine to develop peat beds. Peat forms in two main environments: 1. deposits of plant material, either comprising layers of plant detritus, leaves, sheaves, stems, roots, twigs, branches, and trunks, representing plant material directly accumulated under plant cover, or comprising wholly *in situ* root-structured, (buried) vertical plant stems, mixed with or alternating with horizontally accumulated plant material; these types of peat deposits tend to form root-structured and fibrous peat; and 2. deposits of organic matter, leaves, and other detritus transported to and deposited in deeper water; these types of peat deposits are structureless, or weakly laminated, and have a variable content of diatoms; these latter peat deposits may grade into diatomaceous peat to organic matter rich diatomite. For these latter peats, in extant environments where organic matter is accumulating in deeper water, the surface deposits are water-rich 20–100 cm thick deposits of flocculated organic matter, which grades downwards into an organic matter gel some up to 100 cm thick, which in turn grades into firm peat.

In Western Australia, researchers have informally subdivided peat into fibrous types, and massive or non-fibrous types, essentially implicitly recognising the two depositional environments noted above. However, from the SEM results, it would appear that the category of massive or non-fibrous peat noted by previous workers, in fact, may be partly organic-carbon-rich diatomite or diatomaceous peat. In addition, there is the issue that not all fine-grained black or dark grey sediment are peats. The dark tone to fine-grained sediments may be partly due to organic matter and partly to finely disseminated metal sulphides, particularly iron sulphide.

Peat intraclast gravel and sand form from processes of desiccation or fire. The surface of peats may dry out to form polygonal cracks, and prolonged summer drying and desiccation (particularly if regional water tables are falling during dry phases of climatic cycles), or drying by fire, leads to progressive fragmentation of the cracked surface layer and to the development of angular peat clasts that are incorporated as layers into the peat deposits. In general, peat is most desiccated along the margins of a basin, where drying out will occur first with shrinking of the water body across a basin, or where fires have resulted in the drying-out of these deposits. Once formed, peat clasts may interact with sand bodies that are peripheral to the basin, and during the following wet season, through wave action and sheet wash, they become interlayered with sand.

Calcilutites are dominantly biogenic in origin. While studies elsewhere suggest that carbonate may precipitate inorganically within lakes as calcite, or rarely as Mg-calcite or aragonite (Muller 1971; Muller *et al.*, 1972; Hakanson & Jansson 1983; Tucker & Wright 1990), in this study, particle morphology, microstructure and ultrastructure, and EDS data indicate that the < 63 mm fraction of carbonate particles is dominantly of biogenic origin derived from disintegrated semi-calcareous charophytes and carbonate-impregnated filamentous algae, and comminuted skeletons of calcareous fauna. Also, the range of mineralogy of the tests of invertebrate fauna and charophytes determined by XRD and EDS adequately explains the range of mineralogy of the calcilutites. SEM studies show that while there is some diagenetic precipitation of carbonate within a pre-existing carbonate sediment host (radiating crystals of acicular aragonite embedded in calcilutite exemplify this), and field and laboratory observations show that some calcite is generated by the burning of wood, there has been no evidence for *in situ* chemical precipitation of mud-sized carbonate as intrabasinal sediment. The restriction of carbonate mud largely within limestone terrains, and the chemistry of the wetland waters (*i.e.*, their alkalinity and salinity) indicates that such environments are favourable for charophytes and calcareous fauna which draw on carbonate, bicarbonate and calcium from the groundwaters.

Carbonate skeletal gravel and sand form in wetland basins where there is accumulation of mollusc and other calcareous invertebrate tests. Wave action along wetland margins tends to concentrate accumulations of skeletons into shoreline or nearshore ribbon deposits. Carbonate intraclasts form in wetland basins that have calcilutite and/or carbonate sand deposits. Induration of calcilutite by drying and desiccation (Fig. 4A), followed by fragmentation and reworking, yields simple intraclasts of calcilutite fragments. Cementation by carbonate, and fragmentation of the indurated sheets result in another type of intraformational clast. The host sediment may be calcilutite, skeletal gravel and sand, or earlier-formed intraclast gravel and sand. Cementation during periods of waterlogging and inundation, reworking into fragments during periods of desiccation, transport and rounding during periods of inundation, and re-cementation of clasts and mud deposits during further periods of waterlogging and inundation, generates the intraclast. Repeated cementation and re-working generates complex and polycyclic intraclasts. Reworking by wave action and accumulation of intraclasts into layers and laminae is most common along wetland margins.

Diatomite mainly forms within wetland basins that are located mainly within quartz sand settings in deep water to shoreline environments. Diatomite accumulates as whole to fragmented frustules. At the stage where diatom frustules have become so fragmented that individual particles are smaller than the microstructure of the sieved wall, the sediment no longer is composed of particles that have intergranular porosity, nor do the diatom particles pack within the sediment as a series of randomly oriented plates. This type of sediment has the bulk properties of a quartz silt or a terrigenous clay deposit, and superficially can be mistaken for a terrigenous sediment, since it does not exhibit the properties of traditional porous "diatomaceous earth". This end product of diatom disintegration produces a sediment type similar to white clay or mud which is easily misidentified as a terrigenous deposit. If there are remnants of freshwater sponge spicules in such deposits (noting that normally in studies of stratigraphy and palaeo-sedimentology, the occurrence of sponge spicules implies marine or estuarine environments), these freshwater sediments can also be incorrectly interpreted as an estuarine sediment, *i.e.*, a sponge spicule bearing estuarine clay deposit.

During drying out periods in wetlands, the exposed floor of a diatom deposit in a wetland may be reworked by aeolian processes, transported shoreward, and trapped by peripheral vegetation, to accumulate as shoreline low relief ridges, essentially as shore-parallel supra-littoral to littoral deposits of "mud". Drying out and desiccation of diatomite also leads to the formation of diatomite intraclasts. Thus diatomite intraclast gravel and sand forms within wetland basins, and particularly along their margins, where desiccation has indurated, cracked and fragmented diatomite deposits, and high water conditions have reworked and rounded them to form thin shoreline deposits (Fig. 4B–G). These intraclasts may form clean washed gravel deposits, or may become embedded in a muddy matrix. Intraclasts are embedded in a diatomite matrix where diatom mud, reworked from the wetland margin, or reworked into suspension from basin centres by wave action during high water, is transported shorewards and consequently buries, or is mixed in with, the shoreline intraclasts.

While dominantly marine organisms, sponges are known to be inhabitants of freshwater lakes (Williams 1980). On the Swan Coastal Plain, while they make important contributions to wetland sediments as intrabasinal particles, sponge spicules and their fragments do not become abundant enough to form "spongolites". As noted earlier, generally they comprise < 10% of wetland sediments.

Davis & Rolls (1987) documented freshwater sponges at North Lake, but considered them to be rare in the context of their sampling sites in the urban Perth area. During the surveys of sumplands and the marginal vegetated zone of lakes and sumplands during this study, encrusting sponges were commonly encountered on peripheral vegetation throughout the Swan Coastal Plain, though they were not abundant at a given site. However, the ubiquitous occurrence of sponge spicules and their fragments in the sediments, particularly in the stratigraphic column, suggests that they can make significant contributions to wetland sediments as silica particles beyond their seemingly apparent current rarity in many locations. The extent of their occurrence in the stratigraphic record may be a measure of their greater abundance in the past or an indication of their chemical durability as silica (and hence their increased preservation potential). While organic matter production may overwhelm the surface occurrence of sponge spicules in peat-generating wetlands at the sediment surface, in time, oxidation processes may result in the increase in concentration of spicules relative to organic matter.

Mud-sized phyllosilicate mineral particles commonly are delivered to wetland basins by fluvial processes. However, where there clearly is no major fluvial channel source (as is the case for the isolated wetland depressions bordered by high dunes), or minor fluvial channel (*e.g.*, consequent drainage bordering a basin, and deriving from the adjoining dune high ground), phyllosilicate mud beds in wetlands, and phyllosilicate muddy sand at the base of wetlands derive from wetland margins, bioturbation into the base of the wetlands, and from aeolian sources. The processes whereby fine-grained clay/silt sediment is delivered to the wetland basin is summarised in Figure 17.

In regard to mud-sized phyllosilicate mineral particles derived from the wetland margins or that occurring at the base of the wetlands, the mineralogy of these mud-sized wetland deposits is the same as that coating the yellow sand grains of the surrounding Pleistocene sediments. The stratigraphic array around and under wetlands residing in a yellow sand terrain is as follows:

1. yellow quartz sand underlies the uplands adjoining the wetland basin;
2. prior to the Holocene groundwater inundation yellow quartz sand also formed the floor of the ancestral wetland basin;
3. white quartz sand, leached of its iron oxide content, depleted of its interstitial yellow fine-grained component, and stripped of its clay/silt pellicular envelope, immediately adjoins the wetland basin at levels where either high water tables or the capillary fringe of high water tables interact with the sand;
4. white quartz sand, or grey quartz sand, similarly

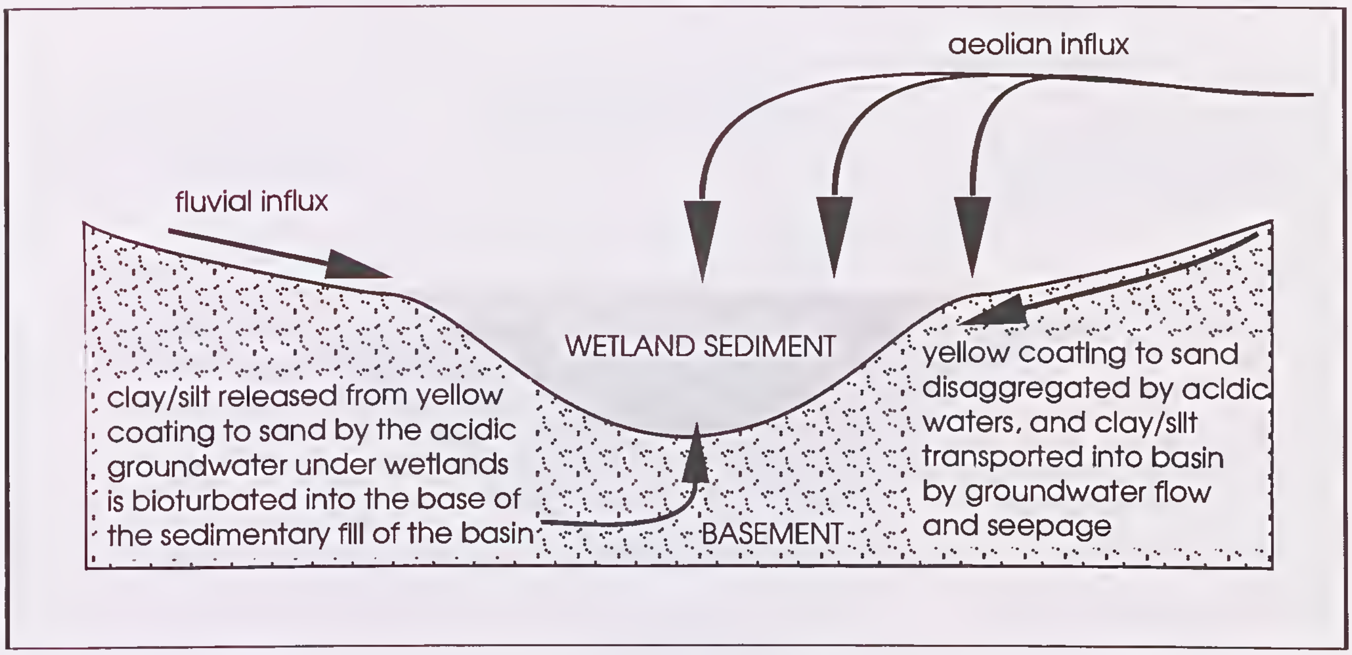

aeolian influx
fluvial influx
WETLAND SEDIMENT
clay/silt released from yellow coating to sand by the acidic groundwater under wetlands is bioturbated into the base of the sedimentary fill of the basin
BASEMENT
yellow coating to sand disaggregated by acidic waters, and clay/silt transported into basin by groundwater flow and seepage

Figure 17. Idealised diagram illustrating the origin of mud-sized phyllosilicate mineral particles in wetland sediments: influx and input from fluvial, sheet-wash, aeolian, groundwater seepage, and (basal) bioturbation processes.

> leached of its iron oxide content, depleted of its interstitial yellow fine-grained component, and stripped of its clay/silt pellicular envelope, underlies the wetland where the sand is permanently or seasonally saturated with water.

In this stratigraphic and hydrochemical setting, yellow sand, proximal to wetlands and water tables, under the influence of acidic groundwater associated with the wetland, or upslope humus-rich soils adjoining wetlands, is bleached white. The clay/silt and iron oxide skins that impart the yellow coating to the quartz grains, and the yellow interstitial fine-grained material are translocated vertically downwards to the water table or laterally to the wetland, or are bioturbated into the base of the wetland. During the wet season, in areas with steep hydraulic gradients, groundwater has been observed seeping into wetlands from the yellow sand margins. Such lateral seepage can carry iron in solution and clay/silt in suspension. In this context, a Pleistocene yellow quartz sand terrain that is host to the wetlands, under conditions of acidic water, in the process of becoming white quartz sand, yields minute amounts of clay/silt and iron oxides. The clay is transported and deposited into the wetland basin. Mud-sized phyllosilicate mineral particles thus can be deposited, albeit in minor amounts, into wetland basins where there is a steep hydraulic gradient into the basin from the adjoining uplands, and this clay/silt can occur in Bassendean Dune and Spearwood Dune settings, since both these Pleistocene dune systems are underlain by yellow quartz sand.

Apart from wetland soils developed directly on Pleistocene quartz sand basement material, the quartz sand that forms sedimentary fill along the margins of wetlands clearly derives from the adjoining uplands (Fig. 4G–H). This is demonstrated by the similarity of the petrography of the quartz grains of wetland fill to those of Pleistocene margins and basement, and by the tracing of the sand sheets and wedges from the wetland basin to the margin. Quartz sand is transported into the wetland margins from the sandy uplands by sheet wash, and the wave reworking of sandy wetland margins during stands of high water. Quartz sand also underlies the beachridge systems that locally form lunettes marginal to some wetlands. However, some of the quartz sand stratigraphically low in the sedimentary profile, near the contact of the accretionary sedimentary fill and the underlying basement sand, derives from bioturbation of the underlying basement sand upwards into the base of the accretionary deposit.

Particles of quartz silt and quartz very fine sand are commonly found scattered in low abundance in central basin deposits of peat, diatomite, and calcilutite. Since there is no fluvial delivery to such basins, and there is no stratigraphic unit that can be traced to the centre of these basins, these fine-grained quartz particles provide evidence of aeolian delivery to wetland basins. The deposits thus consist of accumulating intrabasinal autochthonous wetland sediments with a low volume aeolian air-fall contribution.

A summary of the common wetland sediments encountered in this study, as listed in Table 6, categorised as to primary end-member sediments, mixtures, and secondary (derivative) sediments, and as to how they formed, is provided in Table 7.

Within a given basin, sediments also partition into central deposits, marginal deposits, and basal deposits, or central facies, marginal facies, and basal facies (Fig. 18). The centres of wetlands are more consistently inundated or water saturated, and accumulate peat, diatomite, and calcilutite. The margins of wetlands, with desiccation, cementation, rising and falling of the water table generating extreme wetting and drying, wave action, reworking, sheet wash, and burrowing by vertebrate and invertebrate fauna, preferentially develop

Table 7

Classification of the main wetland sediments and their origin

Sediment	How formed
Primary end-member sediments	
peat	intrabasinal accumulation of plant material
diatomite	intrabasinal accumulation of diatoms
calcilutite	intrabasinal accumulation of disintegrated charophytes and invertebrate skeletons
kaolinitic mud	extrabasinal delivery of fine-grained sediment by fluvial or aeolian processes
quartz sand	extrabasinal delivery of fine-grained sediment by fluvial or marginal sheet wash processes
quartz silt	extrabasinal delivery of fine-grained sediment by fluvial or aeolian processes
skeletal gravel and sand	intrabasinal accumulation of invertebrate skeletons
Secondary (derivative) sediments	
peat intraclast gravel and sand	desiccation, baking, cracking, reworking and accumulation of peat mainly along wetland margins
carbonate intraclast gravel and sand	desiccation, cementation, cracking, reworking and accumulation of carbonate sediments mainly along wetland margins
diatomite intraclast gravel and sand	desiccation, cracking, reworking and accumulation of diatomite mainly along wetland margins
Mixtures of end-member sediments	
peaty quartz sand	mixing by sheet wash or bioturbation of peat and quartz sand either along wetland margins or along the base of the wetland fill; the occurrence of interstitial organic matter indicates that the sediment has formed under anoxic subaqueous or waterlogged conditions
sandy peat	mixing by sheet wash or bioturbation of peat and quartz sand either along wetland margins or along the base of the wetland fill
diatomaceous quartz sand	mixing by sheet wash or bioturbation of diatomite and quartz sand either along wetland margins or along the base of the wetland fill
sandy diatomite	mixing by sheet wash or bioturbation of diatomite and quartz sand either along wetland margins or along the base of the wetland fill
calcilutaceous quartz sand	mixing by sheet wash or bioturbation of calcilutite and quartz sand either along wetland margins or along the base of the wetland fill
sandy calcilutite	mixing by sheet wash or bioturbation of calcilutite and quartz sand either along wetland margins or along the base of the wetland fill
kaolinitic muddy quartz sand and sandy kaolinitic mud	mixing by sheet wash, fluvil processes, or bioturbation of kaolinitic mud and quartz sand either along wetland margins or along the base of the wetland fill
diatomaceous peat	accumulation of organic matter with diatoms, dominated by organic matter
organic matter enriched diatomite and sandy organic matter enriched diatomite	accumulation of organic matter with diatoms, dominated by diatoms
calcilutaceous peat	accumulation of organic matter jointly with calcilutite, dominated by organic matter
organic matter enriched calcilutite and sandy organic matter enriched calcilutite	accumulation of organic matter jointly with calcilutite, dominated by calcilutite
organic matter enriched diatomaceous calcilutite, and sandy organic matter enriched diatomaceous calcilutite	accumulation of organic matter, diatoms and calcilutite
organic matter enriched kaolinitic mud	accumulation of organic matter and kaolinitic mud
organic matter enriched diatomaceous kaolinitic mud	accumulation of organic matter, diatoms, and kaolinitic mud
phytolithic muddy sand	accumulation of phytoliths and mixing of this fine-grained material with sand either by sheet wash or bioturbation along the margins of wetlands

sedimentary structures such as vesicular structures, fenestral structures, breccioid structures, and burrow structures, and the mixing of interlayered sediment. This is the zone where there is development and accumulation of second cycle intrabasinal sediments such as carbonate intraclast gravel and sand, peat intraclast gravel and sand, and skeletal intraclast gravel and sand, and extrabasinal quartz sand aprons and tongues, and marked lithological interlayering between extrabasinal and intrabasinal sediments. During times of exceptionally low water levels, the features of wetland sediments that reflect processes of desiccation and

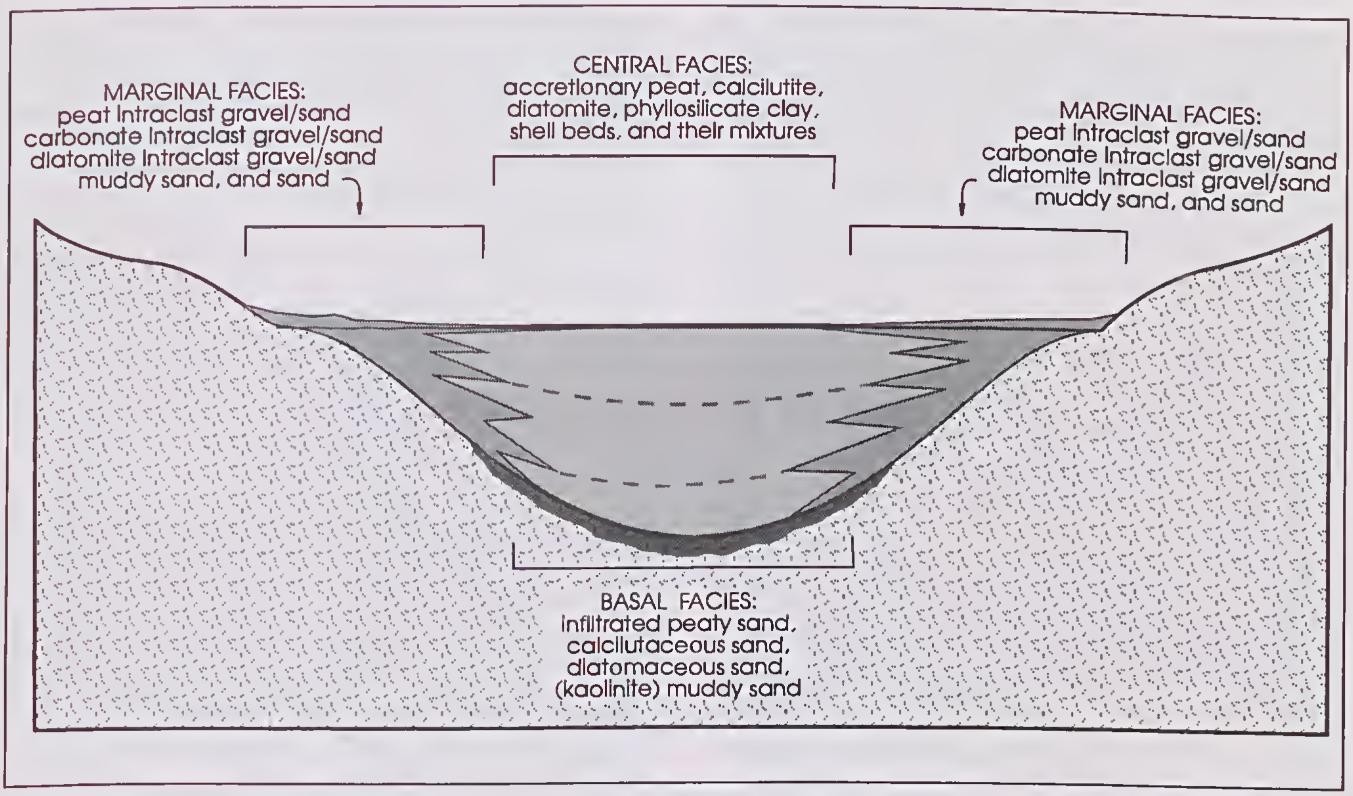

CENTRAL FACIES:
accretionary peat, calcilutite, diatomite, phyllosilicate clay, shell beds, and their mixtures
MARGINAL FACIES:
peat intraclast gravel/sand
carbonate intraclast gravel/sand
diatomite intraclast gravel/sand
muddy sand, and sand
MARGINAL FACIES:
peat intraclast gravel/sand
carbonate intraclast gravel/sand
diatomite intraclast gravel/sand
muddy sand, and sand
BASAL FACIES:
infiltrated peaty sand,
calcilutaceous sand,
diatomaceous sand,
(kaolinite) muddy sand

Figure 18. The major depositional environments of sedimentary particles and wetland sediments as central facies, marginal facies, and basal facies. The relevant sediment types within each facies is listed.

induration along the margins may extend across the entire wetland basin. The term "basal deposits" is applied to the infiltrational deposits at the base of the wetland, and essentially are buried deposits formed at the time of the initiation of wetland sedimentation.

Discussion and conclusions

This is the first systematic and formal description of wetland sediments on the Swan Coastal Plain. As such it provides an inventory of wetland sediment particles, wetland sediment types, a standard set of descriptors to be included in documentation of wetland sediments, and a number of defined terms for future reference. In contrast to soil nomenclature systems that involve classification of combined (segregated) layers in the pedogenic profile, a simple and comprehensive system using sedimentary terms has been employed to describe and classify wetland sediments in this paper, and provide a picture of the internal features of wetland sedimentary deposits, *i.e.*, their colour, structure, fabric, texture, and composition, that can be employed for individual layers in the stratigraphic profile. With descriptors such as intraformational, infiltrational, accretionary, intrabasinal and extrabasinal, information about the genesis of the sediments and nature of the processes of sedimentation can be included, thus further separating sediment types or sediment facies within wetland basins. The descriptive system is not aligned to any single objective, such as agricultural use, and this independence means it may be used as an adjunct in many types of surveys with a variety of purposes.

In this paper, we emphasise that true soils, as pedogenic products on pre-existing parent material, should be distinguished from sedimentary products that are infiltrational and/or accretionary. In the geohistoric reconstruction of wetland development, this is an important factor, and will provide a means of determining the beginning of a wetland's history, in separating deposits that have accumulated as part of the wetland from those materials inherited from pre-wetland conditions (Semeniuk 2005).

In terms of the sediments themselves, a wide range of mud-sized, sand-sized, and gravel-sized sedimentary particles contribute to sedimentary fill underlying wetlands, *viz.*, organic mud particles, microcharcoal and charcoal, carbonate mud particles, quartz sand and silt, diatoms, sponge spicules, mud-sized phyllosilicate minerals (kaolin, montmorillonite), goethite mud, feldspar silt, heavy minerals, intraclasts, shells and fragments, and plant material (plant fibres, detritus, leaves, flowers, fruit, twigs, branches and trunks). Deposits of invertebrate faunal skeletal material, while forming layers and laminae in wetland sediments, do not contribute in a major way to the filling of wetland basins in the settings of the Spearwood Dunes, Bassendean Dunes, and Pinjarra Plain, but can form diagnostic and environmentally significant markers within the sediment suite.

The end-member wetland sediments that are the dominant and/or key intrabasinal and autochthonous on the Swan Coastal Plain are peat, diatomite, and calcilutite. These end-member sediments similarly are recognised globally as being the predominant autochthonous deposits in wetland basins, and as signalling intrabasinal sedimentation. On the Swan Coastal Plain, the occurrence of the end-member sediments and their mixed intermediates reflects geomorphic setting as well as hydrological and hydrochemical setting (see Semeniuk & Semeniuk 2005a), and can be used as environmental indicators when preserved in the stratigraphy. All three of the key end-member sediments are fundamentally biogenic in origin, *viz.*, plant remains generate peat, diatoms generate diatomite, and charophytes and invertebrate fauna disintegrate to form calcilutite. Secondary derivatives of the key primary wetland sediment types, or their intermediates, include the intraclast gravels and sands derived from peat, diatomite, and calcilutite. They are developed most commonly as marginal deposits, as a result of processes of desiccation, cementation, induration, extreme wetting and drying from rising and falling water tables, wave action, or reworking. The effects and alterations of these various processes, although operating in the overall wetland, are most pronounced in the marginal sediments. Extrabasinal, allochthonous terrigenous sedimentary material, within wetlands, such as quartz sand and mud-sized phyllosilicate mineral particles, are delivered to the basins by sheet wash, fluvial transport, and aeolian transport.

Sediments composed of mixed particle types reflect one or more of several processes. They may represent the concomitant production of biogenic material (*e.g.*, diatoms within a peat-generating basin to develop diatomaceous peat; or epiphytic sponges together with plant detritus generating a spongolitic peat), or the biogenic mixing of various sedimentary layers by bioturbation. In lower parts of the stratigraphic section, mixes of sand and muddy wetland sediment may represent infiltrational sedimentation, mediated by bioturbation or gravitational water. On the wetland margins, they reflect the various contributions to the sedimentary accumulation, *e.g.*, extrabasinal allochthonous sediment brought to the wetland by sheet wash, or wave reworking of sandy wetland margins, and mixed with the feather edge of autochthonous sediment deposits generated from within the basin, or aeolian transport of fine-grained sediment from basin centres to basin margins, and the mixing of the fine-grained material with quartz sand adjoining the basin. Some mixes of sediments reflect the bioturbation of formerly interlayered environmentally distinct deposits.

In the light of the classification presented in this paper in Figure 12, and the proposed compositional boundaries within the sediments of the "peat family" between peat *sensu stricto* and diatomaceous or calcilutaceous peat, the nomenclature of peat is discussed further here. In the literature, the terms "peat" and "peaty" is applied to a large range of accreted organic matter, varying in organic content. Some authors define peat quantitatively in terms of organic matter content. For example, Dachnowski (1920) restricts the term to accumulations of plant matter > 20 cm thick and with > 60 % organic matter; in a review of peat, Clymo (1983) notes that the term is generally applied to materials with > 80% organic matter; and Leeper & Uren (1993) attach the term "peaty" to material with organic matter content > 20 %. Many other authors, on the other hand, do not define peat in relation to a quantitative content of organic matter but use the terms "peat" or "peaty" for any organic rich sediment or soils implicitly conveying the notion of rich organic content without quantification or even reference to works that define peat quantitatively. As Clymo (1983) points out, however, "peat" is not a single homogenous substance: it varies in vegetative composition, colour, structure, fabric attributes and proportion of fibre, bulk density and water content, organic matter content, concentration of inorganic solutes, occurrence of mineral precipitates, and extent of decomposition. As such it will have a variable appearance and variable properties dependent on source material, microbial, diagenetic, and pedogenic processes, hydrological setting, hydrochemistry, depth of burial, and age. In this paper, we assign the term "peat" to accreted sedimentary material with > 75% organic matter, varying in structure and fabric from fibrous (partly decomposed plants and detritus) to fine-grained (fully decomposed plants). We place the boundary for peat *sensu stricto* at 75% organic matter for practical reasons in relation to the other subdivisions of the ternary classification (noting though that the 75% threshold is close to the 80% boundary for peat of peatland scientists *cf.* Clymo 1983), and assign organic rich sediments with 50–75% organic matter to the "peat family", but with adjectival descriptors to denote the subdominant constituents in the material.

We also note that iron-sulphide-rich fine-grained sediments may be dark grey or black but not necessarily peat. Iron sulphide rich diatomaceous peat, or iron sulphide and organic matter enriched diatomite, for examples, superficially may resemble peat, and in this context it is necessary either to have determined the organic matter content of the sediment by laboratory analyses, or to have examined the material as mud particle mounts under a petrographic microscope in order to assign the sediment the correct identification.

Generally within wetland basins, carbonate sediments form the most complex suite of products, reflecting diverse biogenic, biomediated, hydrochemical and diagenetic origins, reflecting diverse mineralogic type (*viz.*, calcite, Mg-calcite; aragonite, and dolomite), reflecting the propensity for carbonate mineral species to readily undergo diagenesis, and reflecting hydrochemical and stratigraphic history (von der Borch 1976; Wright 2000; Roberts *et al.*, 2004). In this context, the environmental significance of calcilutites is discussed further here.

Calcilutites, variably known in the literature as lime muds, calcitic muds, aragonitic muds, or carbonate muds, have been documented from a range of aquatic environments in Western Australia and globally. They have been recorded in freshwater to saline hydrochemical systems, from lacustrine to marine environments (Bathurst 1971; Hakanson & Jansson 1983; Wetzel 1983; Hammer 1986; Semeniuk 1988; Backhouse 1993; Newsome & Pickett 1993; Coshell & Rosen 1994). Their mineral composition has been noted as calcitic, Mg-calcitic, and aragonitic, or mixtures of these, and with local dolomite. The origin of the different mineralogic particle types has been determined or interpreted to be biogenic, inorganic precipitations, or diagenetic (Muller 1971; Muller *et al.*, 1972; Kelts & Hsu 1978; Hakanson & Jansson 1983; Tucker & Wright 1990). For lacustrine wetlands, mineralogic types and particle types of calcilutite can be stratigraphically monotonous throughout the wetland sediment sequence. On the other hand, a wide range of carbonate mineralogic types and particle types can occur stratigraphically interlayered or form a graded sequence within the one wetland basin, either because of fluctuating water chemistry, reflecting changing hydrochemical, biotic, and climatic influences, or because of long-term evolving hydrochemistry within the wetland basin, for instance, evolving from freshwater conditions to hypersaline conditions, with attendant long-term changes in biota, hydrochemical processes, and diagenesis (Coshell & Rosen 1994; Machlus 2000).

Against this variable backdrop, the calcilutites within wetland basins on the Swan Coastal Plain encountered in this study are mainly calcitic and mostly derived by breakdown of charophytes and invertebrate biota, and while SEM studies show that there is some diagenetic precipitation of carbonate within a pre-existing carbonate sediment host (radiating crystals of acicular aragonite embedded in calcilutite exemplify this), there has been no evidence for *in situ* chemical precipitation of mud-sized carbonate as intrabasinal sediment. However, in the more saline carbonate basins such as the Coogee Suite or the Cooloongup Suite (Semeniuk 1988), calcilutites exhibit complexity in mineralogy and particle types: there is biogenically derived carbonate mud formed by breakdown of charophytes and invertebrate fauna; there is authigenic precipitation of carbonates formed within the sedimentary body (displacive crystal aggregates, or as crusts and cements of aragonite, Mg-calcite, or dolomite), and there is diagenetic replacement of pre-existing carbonate sediment. These aspects of carbonate sedimentation and diagenesis, however, will be the subject of a later paper.

As noted above, pyrogenesis creates new sediment types, *e.g.*, diatomite, or quartz sand, new textures, and new minerals, but in all cases the process acts on pre-existing sediment. Mostly, pyrogenic processes modify or transform particles within sediments, or create new structures in a pre-existing sediment. In this context, pyrogenesis is viewed as subclass of diagenesis.

The categorisation and description in this paper of wetland sediment types will assist wetland scientists, administrators and planners to address one of the fundamental attributes of wetlands, and indeed, an attribute which defines and delineates wetlands, *i.e.*, "hydric soil" (noting that we use the term "hydric soils" here without implication that all materials that underlie wetlands are wetland "soils"). The limit of "hydric soils" or wetland sediments delineates the boundary of a wetland in combination with two other determining factors, the presence of surface or near surface water, and the presence of hygrophyllic flora or fauna (Tiner 1999). The boundary of a wetland determined by the occurrence of wetland sedimentary deposits, or "hydric soils", becomes increasingly important during periods of natural water level fall, when the characteristics of the water regime such as water presence and longevity are intermittently or cyclically altered or erratic. Wetland sediments are also an important characteristic in wetland inventories and classifications, and in an hierarchical classification system, it is one of the criteria for assigning wetland types to suites (Semeniuk 1988).

The focus on the different sediment end members and mixtures described above, should provide a basis for understanding the dynamic nature of wetlands as they develop, through deepening, infilling, and responding to changes in hydrological and hydrochemical regimes (Semeniuk 2005). Given that many of the sediment types represent particular environmental settings, either in terms of hydrochemistry or location within the basin, *viz.*, centre, or margin of basin, some of the sediment types can be used to infer palaeo-environments and to reconstruct past hydrochemical and climatic conditions. Also, given their strong palaeo-environmental implications, the sediment within a basin also can signal the nature of mechanisms contributing to the current ecological balance, as well as to predict hydrological pathways, recharge and discharge mechanisms, and provide fundamental hydrogeological information critical to the proper design of buffer zones to protect wetlands.

When sediment types are related to geomorphic and geological setting, they can further be used in a predictive capacity to provide clues about the regional and local wetland processes which may be taking place in previously unstudied settings. If sediment types have changed, as evidenced in the wetland fill, this may provide insights into wetland stability and/or identification of potential risk factors.

Wetland sediments provide a powerful tool in the reconstruction of wetland history in the Holocene, particularly if used in conjunction with fauna, flora, pollen, microcharcoal, and diagenetic products. In this context, recognising the sedimentary products of former processes provides an important key to the unravelling of Holocene palaeo-environmental, palaeo-ecological and palaeo-climatic history. For example, the marginal facies represents a distinct hydrochemical and hydrological condition, and such facies recurring as tongues along the wetland margin, or as buried sheets extending across the wetland basin provides information on former wetland conditions. Similarly, the occurrence of shell beds (or laminae), or the incursions of sand into the wetland margin by fluvial processes or by sheet wash, or the regular influx of quartz silt laminae in the stratigraphic sequence by, say, aeolian processes, signal important events in the history of accretion within a wetland, and the recognition of the processes and products of intrabasinal *versus* extrabasinal sedimentation becomes an important part of the stratigraphy of wetlands.

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Appendix 1

Latitude and longitude of the 143 wetland sampling sites and their location in relation to the consanguineous suites of Semeniuk (1988). Sites are mainly ordered from north to south, but also grouped where they are proximal within a given consanguineous suite

Site		Co-ordinates	Suite
1.	Tangletoe Swamp 3	31° 19' 03" S, 115° 45' 04" E	Jandakot
2.	Tangletoe Swamp 1	31° 21' 09" S, 115° 47' 49" E	Jandakot
3.	Tangletoe Swamp 5	31° 21' 22" S, 115° 46' 35" E	Jandakot
4.	Coonabidgee Rd Swamp A	31° 21' 40" S, 115° 49' 46" E	Mungala
5.	Coonabidgee Rd Swamp B	31° 21' 56" S, 115° 51' 49" E	Mungala
6.	Lake Bambum	31° 25' 34" S, 115° 53' 23" E	Mungala
7.	Lake Nambung	31° 26' 02" S, 115° 53' 19" E	Mungala
8.	Lake Mungala 1	31° 26' 18" S, 115° 53' 42" E	Mungala
9.	Lake Mungala 3	31° 26' 29" S, 115° 53' 48" E	Mungala
10.	Bullrush Swamp	31° 29' 29" S, 115° 39' 17" E	Yanchep
11.	Yeal Swamp	31° 28' 17" S, 115° 46' 04" E	Jandakot
12.	Casuarina Swamp	31° 27' 21" S, 115° 46' 22" E	Jandakot
13.	Bullsbrook	31° 37' 39" S, 116° 00' 59" E	Keysbrook
14.	Pinjar Pine Forest 1	31° 37' 06" S, 115° 50' 00" E	Jandakot
15.	Pinjar Pine Forest 5	31° 37' 25" S, 115° 51' 28" E	Jandakot
16.	Pinjar Pine Forest 8	31° 38' 10" S, 115° 53' 04" E	Jandakot
17.	Pinjar Pine Forest 7	31° 38' 58" S, 115° 51' 44" E	Jandakot
18.	Loch McNess	31° 32' 38" S, 115° 40' 51" E	Yanchep
19.	Yonderup	31° 33' 17" S, 115° 41' 09" E	Yanchep
20.	Lake Pippidinny	31° 34' 44" S, 115° 41' 08" E	Yanchep
21.	Lake Carabooda	31° 37' 05" S, 115° 43' 21" E	Yanchep
22.	Lake Nowergup	31° 38' 00" S, 115° 43' 51" E	Yanchep
23.	Lake Pinjar north	31° 36' 12" S, 115° 47' 37" E	Pinjar
24.	Lake Pinjar south	31° 39' 15" S, 115° 48' 11" E	Pinjar
25.	Lake Neerabup	31° 39' 56" S, 115° 44' 49" E	Yanchep
26.	Melaleuca Park (Neaves Rd)	31° 40' 21" S, 115° 54' 15" E	Riverdale
27.	Melaleuca Park diatomite 1	31° 40' 21" S, 115° 53' 45" E	Riverdale
28.	Melaleuca Park diatomite 2	31° 40' 00" S, 115° 53' 38" E	Riverdale
29.	Carramar Swamp	31° 42' 46" S, 115° 46' 22" E	Yanchep
30.	Lake Adams	31° 42' 06" S, 115° 49' 26" E	Gnangara
31.	Lake Joondalup north	31° 43' 03" S, 115° 46' 18" E	Yanchep
32.	Ellenbrook A	31° 43' 26" S, 116° 01' 28" E	Ellen Brook
33.	Pinjar Pine Forest 156	31° 43' 55" S, 115° 56' 53" E	Jandakot
34.	Pinjar Pine Forest 164	31° 43' 38" S, 115° 57' 05" E	Jandakot
35.	Pinjar Pine Forest 88	31° 44' 31" S, 115° 55' 32" E	Jandakot
36.	Pinjar Pine Forest 104	31° 44' 38" S, 115° 55' 49" E	Jandakot
37.	Pinjar Pine Forest 158	31° 44' 13" S, 115° 56' 57" E	Jandakot
38.	Pinjar Pine Forest 132	31° 44' 41" S, 115° 56' 27" E	Jandakot
39.	Lake Jandabup	31° 44' 18" S, 115° 50' 32" E	Gnangara
40.	Lake Mariginiup	31° 43' 29" S, 115° 48' 54" E	Gnangara
41.	Lake Joondalup	31° 44' 32" S, 115° 47' 06" E	Gnangara
42.	Ellenbrook B	31° 44' 13" S, 116° 01' 08" E	Ellen Brook
43.	Ellenbrook C 9	31° 43' 24" S, 115° 57' 29" E	Jandakot
44.	Ellenbrook D1	31° 45' 10" S, 115° 58' 56" E	Jandakot
45.	Ellenbrook D9	31° 45' 14" S, 115° 58' 18" E	Jandakot
46.	Ellenbrook D south	31° 45' 25" S, 115° 58' 25" E	Jandakot
47.	Ellenbrook Swamp North	31° 42' 49" S, 115° 57' 17" E	Jandakot
48.	Ellenbrook Swamp middle	31° 43' 11" S, 115° 57' 11" E	Jandakot
49.	Ellenbrook Swamp south	31° 44' 41" S, 115° 57' 40" E	Jandakot
50.	Sydney Rd Swamp P	31° 46' 57" S, 115° 51' 21" E	Gnangara
51.	Sydney Rd Swamp H	31° 46' 50" S, 115° 51' 15" E	Gnangara
52.	Lake Gnangara	31° 47' 13" S, 115° 52' 11" E	Gnangara
53.	Waluburnup Swamp north	31° 47' 08" S, 115° 48' 14" E	Yanchep
54.	Waluburnup Swamp central	31° 47' 28" S, 115° 48' 25" E	Yanchep
55.	Waluburnup Swamp south	31° 48' 04" S, 115° 48' 40" E	Yanchep
56.	Beenyup Swamp	31° 47' 16" S, 115° 48' 00" E	Yanchep
57.	Lake Goolelal	31° 48' 43" S, 115° 48' 53" E	Yanchep
58.	Yarkin Swamp	31° 47' 38" S, 115° 59' 43" E	Muchea
59.	Waluburnup Swamp	31° 47' 06" S, 115° 48' 13" E	Yanchep

Site		Co-ordinates	Suite
60.	Snake Swamp	31° 48' 00" S, 115° 51' 52" E	Gnangara
61.	Balajura wetlands (now Emu Lake)	31° 50' 25" S, 115° 52' 55" E	Jandakot
62.	Marshall Rd wetland	31° 51' 19" S, 115° 54' 57" E	Bennett Brook
63.	Big Carine Swamp	31° 51' 09" S, 115° 47' 13" E	Balcatta
64.	Little Carine Swamp	31° 50' 52" S, 115° 47' 37" E	Balcatta
65.	Koondoola dampland	31° 50' 55" S, 115° 52' 30" E	Jandakot
66.	Lake Gwelup	31° 52' 43" S, 115° 47' 33" E	Balcatta
67.	Karrinyup Swamp	31° 52' 01" S, 115° 47' 17" E	Balcatta
68.	Karrinyup Road Swamp	31° 53' 26" S, 115° 53' 26" E	Balcatta
69.	Lake Herdsman	31° 55' 12" S, 115° 48' 18" E	Balcatta
70.	Brixton Swamp	32° 01 48" S, 115° 58' 21" E	Mungala
71.	Yule Brook wetlands	32° 01' 16" S, 115° 58' 52" E	Mungala
72.	Kenwick Swamp	32° 02' 21" S, 115° 57' 56" E	Mungala
73.	Canine Swamp	32° 06' 06" S, 115° 56' 05" E	Jandakot
74.	Bull Creek 1	32° 03' 11" S, 115° 51' 32" E	Jandakot
75.	Canning Vale wetlands	32° 03' 16" S, 115° 56' 27" E	Bennett Brook
76.	Piney Lakes	32° 02' 56" S, 115° 50' 11" E	Jandakot
77.	Roe Swamp	32° 05' 01" S, 115° 50' 05" E	Jandakot
78.	North Lake	32° 04' 34" S, 115° 49' 28" E	Bibra
79.	Horse Paddock Swamp	32° 04' 51" S, 115° 49' 26" E	Bibra
80.	Bibra Lake	32° 05' 17" S, 115° 49' 23" E	Bibra
81.	Manning Lake (= Coogee O)	32° 05' 34" S, 115° 46' 18" E	Coogee
82.	Coogee J	32° 07' 52" S, 115° 46' 51" E	Coogee
83.	Lake Coogee (= Coogee G)	32° 08' 15" S, 115° 46' 36" E	Coogee
84.	Lake Coogee South (= Coogee F)	32° 08' 34" S, 115° 46' 59" E	Coogee
85.	Market Garden Swamps	32° 06' 43" S, 115° 46' 42" E	Coogee
86.	Thompsons Lake	32° 08' 52" S, 115° 49' 43" E	Bibra
87.	Lake Forrestdale	32° 09' 33" S, 115° 56' 18" E	Bennett Brook
88.	Banganup Swamp	32° 09' 51" S, 115° 49' 36" E	Bibra
89.	Brownman Swamps West	32° 09' 25" S, 115° 47' 08" E	Coogee
90.	Brownman Swamps East	32° 09' 37" S, 115° 47' 20" E	Coogee
91.	Mt Brown Lake	32° 10' 26" S, 115° 47' 28" E	Coogee
92.	Long Swamp	32° 11' 55" S, 115° 48' 02" E	Coogee
93.	The Spectacles 2	32° 13' 03" S, 115° 50' 19" E	Bibra
94.	Bollard Bullrush Swamp	32° 15' 25" S, 115° 50' 11" E	Bibra
95.	Leda Swamp J	32° 15' 37" S, 115° 48' 46" E	Stakehill
96.	Leda Swamp K	32° 16' 22" S, 115° 48' 26" E	Stakehill
97.	Leda Swamp L	32° 16' 45" S, 115° 48' 34" E	Stakehill
98.	Stakehill A	32° 21' 19" S, 115° 47' 42" E	Stakehill
99.	Stakehill B	32° 22' 25" S, 115° 47' 07" E	Stakehill
100.	Stakehill C	32° 22' 44" S, 115° 47' 28" E	Stakehill
101.	Tamworth Hill Swamp	32° 19' 39" S, 115° 48' 26" E	Stakehill
102.	Anstey Swamp	32° 24' 53" S, 115° 46' 42" E	Stakehill
103.	Pipidinny Swamp	32° 26' 42" S, 115° 47' 05" E	Stakehill
104.	Hammond Rd North Swamp	32° 07' 57" S, 115° 50' 44" E	Jandakot
105.	Hammond Rd South Swamp	32° 08' 07" S, 115° 50' 26" E	Jandakot
106.	Russell Rd Swamp	32° 09' 39" S, 115° 50' 15" E	Jandakot
107.	Twin Bartram Swamp	32° 08' 29" S, 115° 51' 12" E	Jandakot
108.	Emma Treeby Reserve	32° 08' 05" S, 115° 52' 50" E	Jandakot
109.	Orton Road wetland	32° 14' 03" S, 115° 51' 15" E	Jandakot
110.	Mortimer Road wetland	32° 15' 29" S, 115° 51' 27" E	Jandakot
111.	Unnamed basin, near Folly Pool	32° 18' 51" S, 115° 49' 57" E	Goegerup
112.	Wright Lake	32° 06' 01" S, 116° 00' 04" E	Bennett Brook
113.	Piara Swamp	32° 08' 23" S, 115° 55' 22" E	Jandakot
114.	Balfour Rd Swamp 1	32° 05' 50" S, 115° 57' 23" E	Jandakot
115.	Balfour Rd Swamp 2	32° 05' 46" S, 115° 57' 20" E	Jandakot
116.	Balfour Rd Swamp 3	32° 06' 14" S, 115° 57' 15" E	Jandakot
117.	Balfour Rd Swamp 4	32° 06' 31" S, 115° 56' 46" E	Jandakot
118.	Mather Reserve	32° 08' 44" S, 115° 52' 28" E	Jandakot
119.	Shirley Balla Swamp	32° 09' 16" S, 115° 52' 48" E	Jandakot
120.	Forrestdale Road Swamp	32° 07' 51" S, 115° 52' 17" E	Bennett Brook
121.	Forrestdale swamp 1	32° 07' 49" S, 115° 55' 17" E	Jandakot
122.	Forrestdale swamp 2	32° 07' 30" S, 115° 55' 02" E	Jandakot

Site		Co-ordinates	Suite
123.	Forrestdale swamp 3	32° 07' 19" S, 115° 54' 53" E	Jandakot
124.	Kraemer Reserve	32° 08' 44" S, 115° 53' 29" E	Jandakot
125.	Bartram Rd Swamp	32° 08' 43" S, 115° 53' 53" E	Jandakot
126.	Harrisdale Swamp (Green Swamp)	32° 06' 41" S, 115° 55' 35" E	Bennett Brook
127.	Balannup Swamp	32° 06' 49" S, 115° 56' 44" E	Bennett Brook
128.	Balannup-Hale	32° 07' 04" S, 115° 56' 43" E	Bennett Brook
129.	Wright Rd Swamp	32° 08' 17" S, 115° 54' 26" E	Bennett Brook
130.	Wawa Swamp	32° 22' 23" S, 115° 45' 52" E	Becher
131.	Cud Swamp	32° 23' 57" S, 115° 45' 29" E	Becher
132.	West Corio Swamp	32° 32' 32" S, 115° 52' 37" E	Gnangara
133.	North Corio Swamp	32° 32' 18" S, 115° 52' 54" E	Gnangara
134.	Lake Mealup	32° 40' 49" S, 115° 42' 44" E	Bibra
135.	Riverdale wetlands 3	32° 58' 49" S, 115° 47' 37" E	Riverdale
136.	Riverdale wetlands 2	32° 59' 08" S, 115° 47' 39" E	Riverdale
137.	Riverdale wetlands 1	32° 59' 36" S, 115° 48' 03" E	Riverdale
138.	Willie Pool	33° 01' 12" S, 115° 47' 47" E	Riverdale
139.	Kemerton Swamps	33° 07' 22" S, 115° 46' 50" E	Jandakot
140.	Myalup Swamp	33° 07' 57" S, 115° 43' 28" E	Clifton
141.	Mialla Lagoon	33° 09' 59" S, 115° 43' 52" E	Clifton
142.	Benger Swamp	33° 10' 13" S, 115° 50' 09" E	Benger
143.	Burragenup wetland	33° 11' 01" S, 115° 43' 00" E	Clifton

Appendix 2

Description of each of the wetlands from which the 32 wetland sediment standards used in this study: were collected: wetland name, wetland sediment standard number (WSS #), co-ordinates, depth of sample, consanguineous suite and geomorphic setting, type of wetland. The number after a wetland name (*e.g.*, Lake Yonderup 2) refers to one of the study sites within the wetland.

Field name of site (locations ordered north to south); depth of sample; laboratory no	Co-ordinates	Consanguineous Suite and geomorphic setting	Description of wetland
Lake Yonderup 2 10-13 cm WSS-No. 26	31° 33' 17" S, 115° 41' 09" E	Yanchep Suite; karst depressions in swales of Spearwood Dunes	mesoscale linear sumpland
Lake Carabooda 2 10-13 cm WSS-No. 16	31° 37' 05" S, 115° 43' 21" E	Yanchep Suite; karst depressions in swales of Spearwood Dunes	macroscale linear sumpland
Lake Joondalup 0-5 cm WSS-No. 23	31° 43' 03" S, 115° 46' 18" E	Yanchep Suite; karst depressions in swales of Spearwood Dunes	megascale linear lake
Casuarina D 1 0-30 cm WSS-No. 20	31° 27' 21" S, 115° 46' 22" E	Jandakot Suite; basins within star dunes in Bassendean Dunes	mesoscale curvilinear dampland
Pinjar Pine Forest 8v 2-20 cm WSS-No. 33	31° 38' 10" S, 115° 53' 04" E	Jandakot Suite; basins within star dunes in Bassendean Dunes	mesoscale curvilinear dampland
Pinjar Pine Forest 8p 260 cm WSS-No. 34	31° 38' 10" S, 115° 53' 04" E	Jandakot Suite; basins within star dunes in Bassendean Dunes	mesoscale curvilinear dampland
Melaleuca Park 10 cm WSS-No. 18	31° 40' 21" S, 115° 54' 15" E	Riverdale Suite; basins in linear chains between dunes	microscale sumpland with humic muddy sand / mixed coarse and medium sand
Lake Adams 2 0-20 cm WSS-No. 25	31° 42' 06" S, 115° 49' 26" E	Gnangara Suite; basins enclosed by dune ridges	macroscale rounded dampland
Sydney Rd Swamp P 20 cm WSS-No. 11	31° 46' 57" S, 115° 51' 21" E	Gnangara Suite; basins enclosed by dune ridges	microscale rounded dampland
Lake Mungala 1 85 cm WSS-No. 15	31° 26' 18" S, 115° 53' 42" E	Mungala Suite; discharge basins for creeks in the transition zone between Bassendean Dunes and Pinjarra Plain	mesoscale rounded sumpland
Lake Mungala 3 115 cm WSS-No. 8	31° 26' 29" S, 115° 53' 48" E	Mungala Suite; discharge basins for creeks in the transition zone between Bassendean Dunes and Pinjarra Plain	microscale rounded sumpland
Bullsbrook 62-85 cm WSS-No. 13	31° 37' 39" S, 116° 00' 59" E	Keysbrook Suite; gently undulating to flat surface with incised creeks	paluslope to palusplain
Coogee F 1 80 cm WSS-No. 10	32° 08' 34" S, 115° 46' 59" E	Coogee Suite; linear interdune swale underlain by limestone	mesoscale elongate lake
Coogee J 2 65 cm WSS-No. 22	32° 07' 52" S, 115° 46' 51" E	Coogee Suite; linear interdune swale underlain by limestone	microscale ovoid sumpland
Coogee J 3 40-80 cm WSS-No. 9	32° 07' 52" S, 115° 46' 51" E	Coogee Suite; linear interdune swale underlain by limestone	microscale ovoid sumpland
Lake Manning 1 0-5 cm WSS-No. 21	32° 05' 34" S, 115° 46' 18" E	Coogee Suite; linear interdune swale underlain by limestone	microscale ovoid sumpland
Lake Manning 1 100-200 cm WSS-No. 24	32° 05' 34" S, 115° 46' 18" E	Coogee Suite; linear interdune swale underlain by limestone	microscale ovoid sumpland

Field name of site (locations ordered north to south); depth of sample; laboratory no	Co-ordinates	Consanguineous Suite and geomorphic setting	Description of wetland
Leda J 2 45 cm WSS-No. 4	32° 15' 37" S, 115° 48' 46" E	Stakehill Suite; basins within limestone ridges	microscale irregular sumpland
Leda K 1 60-100 cm WSS-No. 7	32° 16' 22" S, 115° 48' 26" E	Stakehill Suite; basins within limestone ridges	microscale ovoid sumpland
Leda K 2 0-30 cm WSS-No. 2	32° 16' 22" S, 115° 48' 26" E	Stakehill Suite; basins within limestone ridges	microscale ovoid sumpland
Leda L 2 40-60 cm WSS-No. 3	32° 16' 45" S, 115° 48' 34" E	Stakehill Suite; basins within limestone ridges	mesoscale irregular elongate sumpland
Stakehill A 1 10-38 cm WSS-No. 14	32° 21' 19" S, 115° 47' 42" E	Stakehill Suite; basins within limestone ridges	mesoscale irregular sumpland
Stakehill A 2 0-60 cm WSS-No. 30	32° 21' 19" S, 115° 47' 42" E	Stakehill Suite; basins within limestone ridges	mesoscale irregular sumpland
Stakehill B 1 60-130 cm WSS-No. 29	32° 22' 25" S, 115° 47' 07" E	Stakehill Suite; basins within limestone ridges	macroscale irregular sumpland
Stakehill B 3 40 cm WSS-No. 28	32° 22' 25" S, 115° 47' 07" E	Stakehill Suite; basins within limestone ridges	macroscale irregular sumpland
Bibra Lake SW 1 0-5 cm WSS-No. 12	32° 05' 17" S, 115° 49' 23" E	Bibra Suite; basins along the contact between the Spearwood Ridges and the Bassendean Sand Dunes	macroscale irregular lake
Banganup Swamp 2 35 cm WSS-No. 5	32° 09' 51" S, 115° 49' 36" E	Bibra Suite; basins along the contact between the Spearwood Ridges and the Bassendean Sand Dunes	mesoscale irregular sumpland
The Spectacles 2 10 cm WSS-No. 19	32° 13' 03" S, 115° 50' 19" E	Bibra Suite; basins along the contact between the Spearwood Ridges and the Bassendean Sand Dunes	macroscale round sumpland
The Spectacles 2 90-110 cm WSS-No. 17	32° 13' 03" S, 115° 50' 19" E	Bibra Suite; basins along the contact between the Spearwood Ridges and the Bassendean Sand Dunes	macroscale round sumpland
West Bollard Bullrush Swamp 35-50 cm WSS-No. 6	32° 15' 25" S, 115° 50' 11" E	Bibra Suite; basins along the contact between the Spearwood Ridges and the Bassendean Sand Dunes	macroscale round sumpland
West Bollard Bullrush Swamp 120-170 cm WSS-No. 32	32° 15' 25" S, 115° 50' 11" E	Bibra Suite; basins along the contact between the Spearwood Ridges and the Bassendean Sand Dunes	macroscale round sumpland
Balannup-Hale 150-175 cm WSS-No. 39	32° 07' 04" S, 115° 56' 43" E	Bennett Brook Suite; Bassendean Dunes with microscale creeks and flats	mesoscale irregular sumpland

Appendix 3

Description of the 32 wetland sediment standards used in this study, in terms of grain size fractions, and particle and crystal composition. om = organic matter; qz = quartz; ph = phytoliths; ss = sponge spicules; ca = undifferentiated carbonate particle; sh = shell; mp = mud-sized phyllosilicate (kaolinite, micas, montmorillonite); di = diatoms; ic = carbonate intraclasts; os = ostracods

Field name of site (ordered north to south); depth of sample; laboratory no	Sediment type	% sand	%mud	Composition of mud by analyses				Visual description under petrographic and stereo-binocular microscope		Comments[3]
				%CO_3 by acid digest	%C by LOI[1]	% residue[2]	Composition by XRD	Sand	Mud	
Lake Yonderup 2 10-13 cm WSS-No. 26	organic matter enriched calcilutaceous muddy sand	46.3	53.7	71.7	15.3	13.0	calcite, quartz, amorphous silica	ic, qz = om	om, ph, di, ss,qz	calcitic carbonate mud with quartz silt and phytoliths, enriched in organic matter is interstitial to a quartz sand frame; XRD detected diatoms, sponge spiculars, and phytoliths as amorphous silica
Lake Carabooda 2 10-13 cm WSS-No. 16	organic matter enriched diatomaceous/ calcilutaceous muddy sand	53.5	46.5	14.0	37.0	49.0	quartz, goethite	om, qz	om > ss, ph, di, mp	mud-sized carbonate skeletal particles, mud-sized phyllosilicate particles, sponge spicules, diatoms and phytoliths occur in the organic matter enriched mud fraction interstitial to a quartz sand frame
Lake Joondalup 0-5 cm WSS-No. 23	organic matter enriched diatomaceous muddy sand	53.4	46.2	26.0	18.4	55.6	quartz, goethite	qz > ss	om > ss > di > mp	mud is interstitial to a quartz sand frame; the amorphous silica in the XRD analysis is diatoms, sponge spiculars, and phytoliths
Casuarina D 1 0-30 cm WSS-No. 20	diatomite	8.5	91.5	2.0	22.0	76.0	quartz, amorphous silica	ss = qz > om	ss & di > qz	XRD and grain mounts of the mud fraction are corroborative in identifying the fine-grained material as quartz silt, diatoms and sponge spicules
Pinjar Pine Forest 8v 2-20 cm WSS-No. 33	sand	82.0	18.0	30.2	1.8	68.0	quartz, microcline, kaolinite, montmorillonite	qz	mp > qz	XRD and grain mounts of the mud fraction are corroborative in identifying the fine-grained material as kaolinite and silt-sized quartz; while classed as "sand", the sediment is moderately kaolinitic muddy, but not as a packstone fabric

Pinjar Pine Forest 8p 260 cm WSS-No. 34	sand	76.7	23.3	10.5	3.2	86.3	quartz, microcline, kaolinite, montmorillonite	qz	mp > qz	XRD and grain mounts of the mud fraction are corroborative in identifying the fine-grained material as kaolinite and other mud-sized phyllosilicate minerals; while classed as "sand", the sediment is moderately kaolinitic muddy, but not as a packstone fabric
Melaleuca Park 10 cm WSS-No. 18	diatomite	19.0	81.0	11.6	4.5	83.9	quartz, amorphous silica	qz & ss > om	ss & di > qz	XRD and grain mounts of the mud fraction are corroborative in identifying the fine-grained material as quartz silt, diatoms and sponge spicules
Adams 2 0-20 cm WSS-No. 25	diatomite	63.9	36.1	8.0	14.2	77.8	quartz, amorphous silica	qz > ss > om	ss & di > qz	XRD and grain mounts of the mud fraction are corroborative in identifying the fine-grained material as quartz silt, diatoms and sponge spicules
Sydney Rd Swamp 20 cm WSS-No. 11	sandy spongolitic diatomite	37.8	62.2	20.0	1.7	78.3	quartz, amorphous silica	qz > ss	di & ss > qz	XRD and grain mounts of the mud fraction are corroborative in identifying the fine-grained material as quartz silt, diatoms and sponge spicules
Lake Mungala 1 85 cm WSS-No. 15	phyllosilicic muddy sand	47.8	52.2	28.0	5.1	66.9	quartz, montmorillonite hydrobiotite	qz	mp > qz > ss	XRD and grain mounts of the mud fraction are corroborative in identifying the fine-grained material as mud-sized phyllosilicate minerals and silt-sized quartz; sponge spicules observed only in grain mount microscopy; sediment is not kaolinitic, hence the general term "phyllosilicic muddy sand"
Lake Mungala 3 115 cm WSS-No. 8	sand	96.1	3.9	27.0	18.5	54.5	quartz, amorphous silica	qz = om (peaty clasts, root, charcoal)	om = ss = qz	sponge spicules detected in the XRD
Bullsbrook 62-85 cm WSS-No. 13	phyllosilicic muddy sand	75.2	24.8	9.0	3.9	87.1	quartz, amorphous silica, montmorillonite, mica	qz	ph > ss > di > qz & mp	sponge spicules and diatoms detected in the XRD; mud-sized phyllosilicate mineral only detected in the grain mounts of the mud fraction; sediment is not kaolinitic, hence the general term "phyllosilicate muddy sand"

Field name of site (ordered north to south); depth of sample; laboratory no	Sediment type	% sand	%mud	Composition of mud by analyses				Visual description under petrographic and stereo-binocular microscope		Comments[3]
				%CO_3 by acid digest	%C by LOI[1]	% residue[2]	Composition by XRD	Sand	Mud	
Coogee F 1 80 cm WSS-No. 10	calcilutaceous muddy carbonate intraclast sand	58.2	41.8	85.0	2.6	12.4	aragonite and calcite, quartz, amorphous silica	ic	ca > ss > om	sponge spicules detected in the XRD; SEM/EDS shows the mud-sized carbonate component to be mixed calcite and aragonite of biogenic origin; quartz silt comprises part of the mud fraction, though not conspicuous in the grain mount microscopy
Coogee J 2 65 cm WSS-No. 22	calcilutaceous muddy carbonate intraclast sand	58.2	41.8	70.5	20.2	9.3	aragonite, calcite, dolomite, quartz, feldspar, goethite, amorphous silica	ic > om	ca > ss > qz	sponge spicules detected in the XRD; SEM/EDS shows the mud-sized carbonate component is mixed calcite and aragonite of biogenic origin, and diagenetic aragonite and dolmite; minor silt-sized quartz and feldspar also present
Coogee J 3 40-80 cm WSS-No. 9	calcilutaceous muddy carbonate intraclast sand	61.2	38.8	78.9	11.0	10.1	quartz, feldspar, amorphous silica, aragonite calcite	ic	ca > ss > om & qz	sponge spicules detected in the XRD; SEM/EDS shows the mud-sized carbonate component is mixed calcite and aragonite of biogenic origin, and diagenetic aragonite; minor silt-sized quartz and feldspar also present
Coogee O 1 0-5 cm WSS-No. 21	(carbonate intraclast) sandy calcilutite	42.4	57.6	80.0	7.9	12.1	calcite, quartz, feldspar, amorphous silica	ic > ph > qz	ca > ss > ph > silt-sized ic	sponge spicules detected in the XRD; SEM/EDS shows the mud-sized carbonate component is calcite of biogenic origin; minor silt-sized quartz and feldspar also present
Coogee O 1 100-200 cm WSS-No. 24	calcilutaceous muddy carbonate intraclast sand	72.3	27.7	91.0	4.6	4.4	aragonite, calcite, quartz, feldspar, amorphous silica	ic = os	NS	sponge spicules detected in the XRD; SEM/EDS shows the mud-sized carbonate component is mixed calcite and aragonite of biogenic origin; minor silt-sized quartz and feldspar also present

Leda J 2 45 cm WSS-No. 4	peaty sand	40.9	59.1	17.1	65.4	17.5	calcite, quartz, amorphous silica	om > qz	om > ss > sh	sponge spicules detected in the XRD; grain mount microscopy corroborates combustion (LOI) results; quartz silt comprises part of the mud fraction, though not conspicuous in the grain mount microscopy
Leda K 1 60-100 cm WSS-No. 7	spongolitic peaty sand	55.6	44.4	10.0	69.5	20.5	amorphous silica	om > qz	om > ss	sponge spicules dominate the amorphous silica component
Leda K 2 0-30 cm WSS-No. 2	sandy calcilutite	35.8	64.2	77.6	14.7	7.7	calcite, quartz, amorphous silica	sh, os > om > qz	om > ss > qz & sh	calcite of biogenic origin; XRD detects sponge spicules; quartz silt comprises part of the mud fraction
Leda L 2 40-60 cm WSS-No. 3	sandy diatomaceous peat	27.1	72.9	11.4	71.4	17.2	quartz, calcite, amorphous silica	om > sh > qz	om > ss > sh	calcite of biogenic origin; XRD detects sponge spicules; quartz silt comprises part of the mud fraction, though not conspicuous in the grain mount microscopy
Stakehill A 1 10-38 cm WSS-No. 14	sandy organic matter enriched diatomaceous/ calcilutaceous mud	24.7	75.3	42.0	25.2	32.8	calcite, quartz	qz > sh	sh > ss > om	calcite of biogenic (shell) origin; quartz silt comprises part of the mud fraction, though not conspicuous in the grain mount microscopy
Stakehill A 2 0-60 cm WSS-No. 30	organic matter enriched diatomaceous/ calcilutaceous muddy sand	64.6	35.4	46.0	36.3	17.7	calcite, quartz, amorphous silica	om > sh > qz	ca, sh > om > ss	calcite of biogenic (shell) origin; quartz silt comprises part of the mud fraction, though not conspicuous in the grain mount microscopy
Stakehill B 1 60-130 cm WSS-No. 29	sandy peat	11.4	88.6				calcite, quartz, amorphous silica	ic > sh > qz	sh > om > ss	calcite of biogenic origin; XRD detects sponge spicules
Stakehill B 3 40 cm WSS-No. 28	organic matter enriched calcilutaceous muddy sand	47.5	52.5	74.3	16.5	9.2	calcite, quartz, amorphous silica	os & sh > qz > om	sh > om > ss	calcite of biogenic origin; XRD detects sponge spicules; quartz silt comprises part of the mud fraction
Bibra Lake SW 1 0-5 cm WSS-No. 12	organic matter enriched diatomaceous muddy sand	64.4	35.6	10.0	30.4	59.6	quartz, amorphous silica	om > ss > qz	om > di > ss > qz	calcite of biogenic origin; XRD detects sponge spicules and diatoms; quartz silt comprises part of the mud fraction
Lake Banganup 2 35 cm WSS-No. 5	sandy spongolitic organic matter enriched diatomaceous kaolinitic mud	16.5	83.5	8.1	24.2	67.7	quartz, kaolinite, amorphous silica	om > ss > qz	mp, ss, om	XRD and grain mount microscopy corroborate kaolinite as the dominant ineral in the mud fraction; quartz silt comprises part of the mud fraction

Field name of site (ordered north to south); depth of sample; laboratory no	Sediment type	% sand	%mud	Composition of mud by analyses				Visual description under petrographic and stereo-binocular microscope		Comments[3]
				$\%CO_3$ by acid digest	%C by LOI[1]	% residue[2]	Composition by XRD	Sand	Mud	
The Spectacles 2 10 cm WSS-No. 19	organic matter enriched diatomaceous muddy sand	58.8	41.2	11.3	6.0	82.7	quartz, amorphous	qz > ss = om	di > ss > qz	XRD detects sponge spicules and diatoms and corroborates grain mount microscopy; quartz silt comprises part of the mud fraction
The Spectacles 2 90-110 cm WSS-No. 17	sandy spongolitic kaolinitic diatomite	10.8	89.2	9.5	5.6	84.9	quartz, amorphous silica, kaolinite	ss = qz > om	ss > di > qz > om > mp	XRD detects sponge spicules and diatoms; grain mount microscopy corroborates XRD that kaolinite and silt-sized quartz occur as mud fraction mineral
West Bollard Bullrush Swamp 35-50 cm WSS-No. 6	sandy spongolitic phyllosilicic diatomite	39.0	61.0	6.9	9.7	83.4	quartz, feldspar, sericite	z > om	ss = di > qqz = om > mp	XRD detects sponge spicules and diatoms; grain mount microscopy corroborates XRD information that phyllosilicates and silt-sized quartz occur as mud fraction minerals; the mud fraction of this sediment is a spongolitic phyllosilicic diatomite
West Bollard Bullrush Swamp 120-170 cm WSS-No. 32	spongolitic phyllosilicic muddy sand	43.5	56.5	17.5	8.2	74.3	quartz, calcite, feldspar, mica, sericite	qz > sh > om	ss > qz > mp	only grain mount microscopy recorded sponge spicules; silt-sized feldspar, quartz, and micas occur in the mud fraction
Balannup-Hale 150-175 cm WSS-No. 39	kaolinitic muddy sand	77.5	22.5	8.0	5.2	86.8	quartz, feldspar, montmorillonite, kaolinite	qz	mp > qz	grain mount microscopy corroborates XRD information that phyllosilicates and quartz silt occur as mud fraction minerals

1. LOI at 550° C mostly removes carbon in organic matter
2. residue after acid digestion, and loss of organic matter by LOI consists of biogenic silica, mud-sized phyllosilicate minerals, quartz, other minor siliciclastic particles, oxidised metal sulphides (e.g., goethite, haematite), and the ash from organic matter (viz., sulphates and chlorides of Na, K, Ca, and Mg)
3. bearing in mind that the % residue after acid digestion and LOI is comprised of primary sedimentary particles, diagenetic particles, and residues generated as ash after combustion, the composition of the mud sized fraction is based on information on % carbonate (determined by acid digestion), % carbon (determined by LOI), % residue, and grain mount microscopy

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Introduction of redclaw crayfish *Cherax quadricarinatus* (von Martens) to Lake Kununurra, Ord River, Western Australia: prospects for a 'yabby' in the Kimberley

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Abstract

The recent introduction of redclaw crayfish for aquaculture to the Ord River region of Western Australia has been followed by the detection of a 'wild' population in Lake Kununurra. A gut survey of the lake's fish fauna was used to estimate the degree of assimilation of redclaw crayfish into the lake's food chain, however very few crayfish were found in only two catfish species (Ariidae). These results leave us uncertain of whether this low detection rate is due to either low numbers of redclaw crayfish in the lake, or that alternative food resources in the lake means that predation of redclaw crayfish is either due to opportunism or is of dietary insignificance. A further possibility is that the survey was undertaken at a time too soon to allow redclaw establishment and assimilation into the lake ecosystem. Whichever, translocating non-endemic freshwater crayfish into novel environments inevitably raises the possibilities of competitive interactions between the introduced and endemic species, food web alterations via predation and grazing pressure, the addition of symbionts, habitat alterations, and disease introductions. An account of how the introduction of a non-endemic crayfish causes all or some of these problems is yet to be adequately described in Australia, however there is an urgent need for such an assessment and the opportunity is now available at Lake Kununurra.

Keywords: redclaw crayfish; *Cherax quadricarinatus*; introduced species; translocation

Introduction

The redclaw crayfish *Cherax quadricarinatus* (von Martens) is a physically robust species that grows relatively quickly in a wide range of environments (Jones & Ruscoe 2001). Redclaw crayfish typically breed annually during the spring/summer months, although recurrent spawning has been observed in at least some females (King 1993; Barki *et al.* 1997). Females are moderately fecund (King 1993; Austin 1998) and incubate their eggs until hatching of highly developed juveniles (Jones *et al.* 2000).

In Australia, the pre-European distribution of redclaw crayfish is thought to be confined to the ephemeral catchments of far northern Queensland and the northern and eastern parts of the Northern Territory (Riek 1969; Curtis & Jones 1995), however the significant aquaculture potential of this species (see Jones *et al.* 2000) has resulted in them being widely translocated within Australia and overseas (Horwitz 1990; Curtis & Jones 1995). There are no known native freshwater crayfishes in the Kimberley region of Western Australia's far north (Riek 1967,1969; Jasinska *et al.* 1993) and redclaw crayfish is classified as a restricted fish species for importation into Western Australia (Anon 1997). In 1998, the Western Australian Department of Fisheries (WADF) introduced a small population of the selectively improved 'Walkamin' strain of redclaw crayfish (see Jones *et al.* 2000) to a quarantine station near the northeast Kimberley town of Kununurra, to determine its suitability for aquaculture in the Ord River Irrigation Area (ORIA). Following a quarantine period of about 12 months, the Walkamin stock were certified as 'disease-free' by WADF personnel and redclaw crayfish aquaculture licences were issued to a few farms in the ORIA. In 2000, 'wild' redclaw crayfish were first found in Lake Kununurra (R. Doupé unpub data; D. Harvey, WADF, pers comm), a Ramsar listed irrigation water supply reservoir on the Ord River (Fig 1). Initial speculation was that the animals had escaped from aquacultures in the ORIA, but a comparative investigation of the genotypes of Lake Kununurra redclaw and a range of redclaw genotypes from elsewhere by Greenway & Mather (2000), indicated that these animals were not of the 'Walkamin' strain, but were more closely related to Northern Territory redclaw crayfish populations; the exact population has never been identified. Who translocated redclaw crayfish to Lake Kununurra is unknown, however in the time since their detection, officers of the Australian Quarantine and Inspection Service have occasionally confiscated redclaw crayfish from recreational fishermen attempting to bring these animals from the adjacent Northern Territory into the Kimberley for use as fish bait (T. Thorne, WADF, pers comm).

There are significant risks associated with the movement of aquatic species by human agency. For example, translocating freshwater crayfish into novel environments raises the possibilities of competitive interactions between the introduced and endemic species (including epibiotic species associated with the crayfish themselves), food web perturbations, habitat alterations, and disease introductions (Horwitz 1990; Holdich 1999; Lodge *et al.* 2000). There may be an increased likelihood that translocated redclaw crayfish could escape and contribute to these types of ecological impacts because their propensity to climb and move out of the water means that they are very difficult to contain (Jones *et al.* 2000). How many redclaw crayfish are now in Lake Kununurra or adjacent waterways is also unknown, but given the potential ecological problems associated with the translocation of freshwater crayfish (and aquatic species generally, see also Doupé & Lymbery 2000; Morgan & Gill 2001; Morgan *et al.* 2002), this introduction should not be ignored. Indeed, Lake Kununurra and the greater Ord River system has been, and continues to be, subjected to a variety of proposed species introductions (*e.g.* Doupé & Bird 1999; Doupé & Pettit 2002; Doupé *et al.* 2005) and escapement from aquacultures (Doupé & Lymbery 1999).

Relatively high fecundity, mobility to invade new habitats, and the ability to compete for available resources, are prominent ecological attributes commonly shared by successful invaders (Elton 1958; Fox & Adamson 1986). Nevertheless, the single-most significant factor affecting their eventual distribution in the new environment concerns the level of ensuing predation of them by resident species (Krebs 1985), and from that end, food webs can form a useful starting point for the theoretical analysis of community organisation (Cohen 1978; Pimm 1982). In this paper, we present the results of a preliminary survey intended to investigate the extent to which redclaw crayfish have thus far been assimilated into the Lake Kununurra ecosystem using a gut survey of the resident fish community. We use those findings to provide a baseline for future research on redclaw crayfish distributions, and to discuss the potential impacts of introducing redclaw crayfish to the waterways of the Kimberley region.

Materials and Methods

The irrigation water supply reservoir of Lake Kununurra (128°46'E 15°57'S) is a very large, linear wetland approximately 55 km long and with a full supply surface area of about 100 million m^2. During daylight hours in December 2002, we surveyed the fish fauna of Lake Kununurra by sampling 12 recognisably different habitats in the lake proper and associated lagoons, and six sites in a major side-creek that connects Lake Kununurra to Lake Argyle (*i.e.* Spillway Creek; see Fig 1). Fishing gear comprised monofilament gill nets (50, 100, 125, 150 and 200 mm stretched mesh width), seine nets (5 and 15 m nets of 3 mm woven mesh width), and rod and line. On capture, all fish were identified and counted.

We also collected 38 lesser salmon (or blue) catfish *Arius graeffei* Kner & Steindachner from one site in Lake Argyle and 56 lesser salmon catfish and 20 barramundi *Lates calcarifer* (Bloch) from three sites in the lower Ord River (approximate locations are given in Fig 1), and whole guts were checked only for the presence of redclaw crayfish remains.

For fishes taken from Lake Kununurra, between 6 and 60 individuals of each species were retained for dietary analyses. The whole stomach was removed for dietary examination, and diets were analysed using the frequency of occurrence (Hynes 1950) and points (Ball 1961) methods; the frequency of occurrence method represents the incidence with which a particular prey type is consumed by a species, whereas the points method gives the relative contribution of each prey type to the total volume of the stomach contents.

Results

Of the 19 fish species collected from Lake Kununurra (see Gill *et al.* 2005), the guts of the freshwater longtom *Strongylura krefftii* (Günther), black catfish *Neosilurus ater* (Perugia), and Macleay's glassfish *Ambassis macleayi* (Castelnau) were empty, and because only three northern trout gudgeon *Mogurnda mogurnda* and a solitary sleepy cod *Oxyeleotris lineolatus* (Steindachner) were collected, dietary data for these species were not recorded. Morgan *et al.* (2004) provide a detailed description and discussion of the component diets of all species.

Claw remnants of redclaw crayfish were found in both the lesser salmon catfish and silver cobbler *A. midgleyi* Kailola & Pierce taken from Lake Kununurra. The frequency of occurrence of redclaw crayfish in the guts of each species was 3.57% and 8% respectively, and this low rate was reflected in a correspondingly small contribution of redclaw crayfish to the total stomach volume of each (2.84% and 7.97% respectively). We also found remains of another decapod, the endemic freshwater prawn or cherabin *Macrobrachium* sp., in the guts of lesser salmon catfish, silver cobbler, barramundi, and Jenkins' grunter or black bream *Hephaestus jenkinsi* (Whitley). Cherabin frequently occurred in the guts of lesser salmon catfish (32.14%) and barramundi (29.79%), and to a lesser extent in Jenkins' grunter (14.81%) and silver cobbler (12%), but contributed significantly less to the total gut content of lesser salmon catfish (7.15%) and Jenkins' grunter (1.10%) than for either silver cobbler (10.95%) or barramundi (26.42%).

No redclaw crayfish were found in either lesser salmon catfish or barramundi taken from Lake Argyle or the lower Ord River, however most guts of both species from all sites contained remnants of cherabin and other species of teleost.

Discussion

Considering that redclaw crayfish was found in very low numbers in lesser salmon catfish and silver cobbler, and contributed similarly low levels to the total volume of their guts, do these results mean that, (1) there are few redclaw crayfish in Lake Kununurra? (2) Predation of redclaw crayfish by these catfishes is a relatively opportunistic event? And/or (3), that the time of sampling (*i.e.* late 2002) was too soon post-discovery to establish the extent to which redclaw have been assimilated into the lake ecosystem? We are also unsure of the significance of redclaw crayfish to the diets of lesser salmon catfish or silver cobbler, or indeed other fish species of the lake; we expect that barramundi would also predate

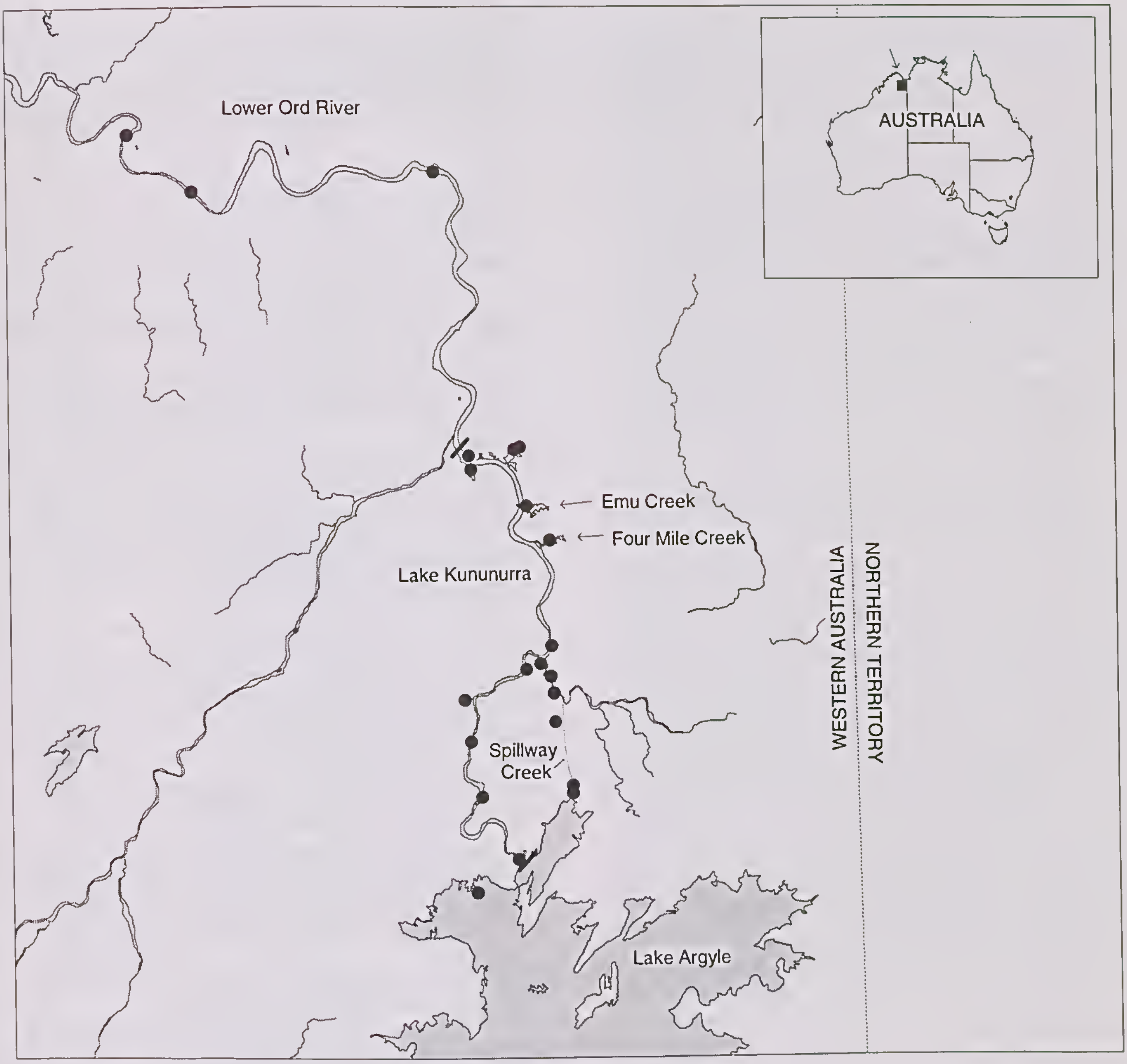

Figure 1. Lake Kununurra in the Ord River system and positions of study sites (●).

on redclaw crayfish, although we only caught four individuals because very few barramundi are found in Lake Kununurra as a consequence of damming (Doupé & Bird 1999).

Lesser salmon catfish and silver cobbler were collected at nine sites in Lake Kununurra and six sites in Lake Argyle, and redclaw crayfish were detected only in samples taken from these two species in the lagoons of Emu Creek and Four Mile Creek (see Fig 1). No evidence of redclaw was found in gut examinations of 94 lesser salmon catfish and 20 barramundi sampled outside of Lake Kununurra; we are therefore uncertain of the distribution of redclaw crayfish in either Lake Kununurra or the greater Ord River system, however we are aware of redclaw crayfish being caught at the lower end of Lake Kununurra (A. Storey, UWA, pers comm.; R.Doupé unpub data).

What are the likely impacts of introducing a crayfish to a water body where the resident community has (presumably) evolved in their absence (*sensu* Horwitz 1990; Jasinska *et al.* 1993; Horwitz & Knott 1995; Lynas *et al.* 2004)? Lamentably we are presently unable to answer this question for Lake Kununurra, however we have a number of concerns. For example, in southwestern Australia, introduced *Cherax* have shown aggressive and predatory behaviour toward congenerics (see Austin & Ryan 2002; Molony *et al.* 2002) and aquatic vertebrates (Bradsell *et al.* 2002), and Fernendez & Rosen (1996) documented similar antagonistic behaviour toward aquatic reptiles by introduced virile crayfish *Orconectes virilis* (Hagen). Jones & Ruscoe (2001) have described redclaw crayfish as "gregarious" in a crowded monoculture, but what might we anticipate when Lake Kununurra suddenly has an extra decapod? In North

America, the introduction of rusty crayfish *Orconectes rusticus* (Girard), presumably for recreational fishing (Horwitz 1990), is believed to be responsible for the decline of two endemic conspecifics, *O. propinquus* (Girard) and *O. virilis* (Hagen)(Lodge *et al.* 1985). Moreover, competitive displacement can occur even between endemic conspecifics if the range of one expands; in southwestern Australia, the spread of smooth marron *C. tenuimanus* (Smith) has resulted in a rapid decline in the population size and distribution of the highly restricted hairy marron *C. cainii* Austin (Austin & Ryan 2002). The redclaw crayfish mostly feeds on detritus and zooplankton (Loya-Javellana *et al.* 1993), and is able to survive and persist in a wide range of habitats (Jones *et al.* 2000), but what effect will it have on its new environment? The extensive burrowing behaviour of the introduced 'yabby' *C. destructor* (or *C. albidus*)(Clark) alters aquatic habitat (Austin 1985) and is thought to contribute to the displacement of native crayfish species such as smooth marron (Lynas *et al.* 2004).

Identifiable remnants of redclaw crayfish taken from fish guts were sent to P. Mather of the Queensland University of Technology for microsatellite gene screening, however DNA extraction (see Baker *et al.* 2000) was unsuccessful and we were unable to determine the genetic origins of those samples. It is important, nevertheless, that we understand how these animals are entering Lake Kununurra and if they are dispersing throughout the Ord River system, because freshwater crayfish harbour a wide variety of symbiotic or parasitic organisms, including bacteria, fungi and parasitic worms (see descriptions in Herbert 1987; Horwitz 1990; Gelder 1999). Following, if these animals are being translocated from wild populations, then what other invertebrates are also being introduced? Alternately, if these animals are escapees from aquacultures, 'disease-free' status should not necessarily diminish concerns for the potential introduction of deleterious symbionts, because presumably, such a certification is limited *a priori* in what is a 'disease'? Some recent Australian work has discovered some disturbing associations between cultured redclaw crayfish and the prevalence of infectious diseases. For example, rickettsia-like parasites have been explicitly linked to a variety of infectious diseases in humans and other vertebrates (Romero & Jimenez 2002), and these organisms have been found in a number of redclaw crayfish aquacultures in Queensland where the crayfish is thought to act as an intermediate host (Edgerton & Prior 1999). At another Queensland redclaw crayfish farm, viral infections characteristic of the Parvoviridae have caused mass mortalities and have again raised concerns for the potential spread of diseases by redclaw crayfish (Bowater *et al.* 2002).

We are unaware of any documented accounts in Australia of where the introduction of a non-endemic tropical crayfish has caused either the displacement or elimination of native freshwater species or changes in aquatic communities. However, the nature of crayfish and particularly their associations with a wide variety of organisms, suggests that there are justifiable reasons to be concerned with any translocation of them, regulated or not. The opportunity to understand better the potential impacts of a redclaw crayfish introduction now presents itself at Lake Kununurra.

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